

INFLUENCE OF CHANGES IN FRESHWATER FLOW ON THE USE OF
MANGROVE PROP ROOT HABITAT BY FISHES

By

JANET A. LEY

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TABLE OF CONTENTS

	<u>Page</u>
ACKNOWLEDGEMENTS.....	ii
ABSTRACT.....	viii
CHAPTERS	
1. GENERAL INTRODUCTION.....	1
Estuarine Fish Ecology.....	1
Mangrove Fish Ecology.....	3
The Florida Bay Ecosystem.....	5
Problem Definition.....	9
Objectives.....	12
Study Area.....	13
Fish Community Sampling Design.....	14
2. FISH DENSITIES AND ASSEMBLAGE PATTERNS IN MANGROVE HABITATS: COMPARISONS ACROSS SALINITY GRADIENTS.....	17
Materials and Methods.....	19
Results.....	32
Discussion.....	84
3. FISH COMMUNITIES IN FLORIDA BAY MANGROVE SHORELINE HABITATS: RELATIONS WITH PHYSICAL PARAMETERS AND COVER.....	98
Materials and Methods.....	99
Results.....	109
Discussion.....	114
4. FOOD HABITS OF MANGROVE FISHES: A COMPARISON ACROSS SALINITY GRADIENTS.....	120
Materials and Methods.....	121
Results.....	123
Discussion.....	129
5. PREDATOR ENCOUNTER RATES ON SMALL BENTHIC FISH ACROSS A SALINITY GRADIENT.....	134
Materials and Methods.....	137
Results.....	143
Discussion.....	149

6.	IMPLICATIONS AND CONCLUSIONS.....	154
	Implications for Mangrove Fish Ecology.....	154
	Implications for Estuarine Fish Ecology:	
	the Nursery-ground Hypothesis.....	157
	Management Implications.....	158
	LITERATURE CITED.....	161
	BIOGRAPHICAL SKETCH.....	172

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By Janet A. Ley

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Chairperson: Clay L. Montague

Cochairperson: Carole C. McIvor

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The hypothesis that seasonal changes in freshwater inflow (indicated by salinity) influence habitat use by fishes was tested in northeastern Florida Bay, extreme south Florida. Fishes were sampled monthly for 13 months using visual censuses and enclosure nets.

Of the 305,589 individuals observed, 91% were estuarine residents, numerically dominated by engraulids, atherinids and cyprinodontids. Occasional marine and freshwater visitors comprised 2% of the individuals, and estuarine transients, 8%. No young-of-the-year estuarine transients were observed.

Salinity ranged between 0.0 to 58 parts per thousand (ppt) upstream, 19.5 to 54 ppt midstream, and 30 to 50 ppt downstream. The 77 species were grouped for analysis:

small benthic, small water column, and larger fishes. Abundances of larger fishes were consistently lower upstream (0.15 fish/square meter (m^2)), than mid- (0.65 fish/ m^2), or downstream (0.55 fish/ m^2). Species of larger fishes numbered fewer upstream (11), than midstream (15), and downstream (22). Benthic and water column fish abundances did not vary along the gradient. Temporally, fish distribution was uncorrelated with salinity.

Development of mangrove habitat and submerged aquatic vegetation (SAV) were reduced upstream. Fish diets shifted to other foods upstream. Thus, where seasonal changes in freshwater inflow were greater (i.e. upstream), species and numbers of larger fishes were lower, possibly due to salinity conditions, food availability and habitat development.

To determine if lower salinity conditions alone led to reduced predation, prey fishes were tethered along the gradient. Predator encounter rates were not different over the salinity range tested, but were 50% lower at the most remote sites. This was perhaps a function of accessibility of the sites to roving predators.

Water management strategies to increase mangrove development and SAV are recommended research priorities. However, severe ecotonal differences between Bay and ocean waters, coupled with limited circulation and significant

predation may inhibit recruitment and survival of post-larval fishes from offshore. An unbroken continuum of good habitat from outer to upper reaches may be necessary if northeastern Florida Bay is to function as a prime nursery area for estuarine transient fishes.

CHAPTER 1 GENERAL INTRODUCTION

The goal of improved management of surface waters to benefit estuarine fish populations in Florida Bay provided the incentive for this research. Before objectives and strategies can be established toward this goal, however, a better understanding of how freshwater inflow influences fish communities in mangrove estuaries overall is needed. This involves aspects of fish ecology of both estuarine and mangrove ecosystems.

Estuarine Fish Ecology

Ecologists often divide estuarine fishes into three groups: estuarine residents (complete their entire life cycle in the estuary), estuarine transients (spawn offshore, their young use the estuary as a nursery), and occasional marine visitors (usually adults) (Day et al. 1989). Resident and transient species tend to be widespread, but marine visitors are usually restricted to the higher salinity zones of the lower estuary (Weinstein 1979). At certain times of the year densities may increase dramatically as influxes of transient juveniles enter estuarine systems. Some species tend to migrate to upstream-most habitats upon initially entering the estuary;

they then may disperse to lower reaches as they grow larger (Weinstein 1979, Rogers et al. 1984, Loneragan et al. 1990).

The prominence of transient juvenile fish and crustaceans led to the application of the term "nursery-ground" to many estuaries (Gunter 1961, McHugh 1967, Weinstein 1979). A major role of freshwater discharge in such systems may be to increase food availability for fishes by transporting nutrients which stimulate primary production and by increasing detrital transport and processing (Odum et al. 1982). Freshwater inflow may also improve the chance for survival of juvenile fish in estuaries by reducing salinity levels below the limits tolerable by stenohaline marine predators (Gunter 1961, 1967).

Browder and Moore (1981) offered a comprehensive nursery ground hypothesis linking several of these concepts. They split habitat factors into those that are relatively stable (e.g. shoreline edge, bottom type) and those that are movable (e.g. salinity, food resources). Favorable habitat for particular juveniles consists of combinations of these factors that promote growth. According to their theory, the inflow of freshwater acts to position an area of favorable moveable habitat relative to important stationary habitat. Thus, for any estuary there is a rate of freshwater flow sufficiently high to push the band of potentially favorable moveable features beyond estuarine boundaries into open waters, perhaps eliminating favorable habitat entirely. Likewise, for every estuary, there is a rate of freshwater

flow so low that the band of favorable salinities retreats upstream where stationary features may be unfavorable. The ideal situation with regard to freshwater inflow is one that maximizes the area of favorable habitat within the estuary over the peak period of nursery use. This hypothesis seems particularly applicable for analyses of fish ecology in mangrove-dominated estuaries.

Mangrove Fish Ecology

In tropical and subtropical areas of the world, mangroves are dominant shoreline features. Mangrove-derived detritus forms a food base for fish occupying mangrove ecosystems (Odum 1971). Mangrove shorelines may also provide cover for fishes (Thayer et al. 1987a). However, few studies have documented aspects of the direct use of mangrove habitats by fishes probably because monitoring fishes within the complex tangle of roots and branches is extremely difficult. Efforts have only recently focused on obtaining quantitative data on habitat use (i.e. Thayer et al. 1987a, Sheridan 1991, Morton 1990, Robertson & Duke 1987). Strong linkages between mangroves and adjacent habitats may exist. For example, diel habitat shifts occur in both non-tidal (Thayer et al. 1987a) and tidal systems (Morton 1990, Robertson & Duke 1987). Shifts from other habitats to mangroves occur during the life history of some species such as gray snapper (*Lutjanus griseus*) (Starck & Schroeder 1971).

The degree of selection among mangrove habitats by fishes has not been determined. Due to variation within mangrove forests, however, preferences are likely to be displayed. In south Florida, for example, three species of mangrove trees occur: red mangroves (*Rhizophora mangle*), black mangroves (*Avicennia germinans*) and white mangroves (*Laguncularia racemosa*) (Odum et al. 1982). These trees vary greatly in type of submerged features and potential cover for fishes. For example, red mangroves provide prop-roots; these are strong, woody structures that tend to extend from the mid-tree trunk downward to the substrate. Black mangroves, in contrast, tend to support a bed of pneumatophores that are pencil-like structures that grow upward from the substrate to several centimeters.

Variation in degree of exposure to flushing also contributes to differences among mangrove forests and, hence, may influence habitat use by fishes. While the fringing mangroves along the shoreline are regularly flooded and thus accessible, more interior basin forests are irregularly inundated and thus occasionally available (Odum et al. 1982).

Within fringing shorelines, higher flushing rates contribute to greater mangrove habitat development (e.g. taller trees, more leaf production), which, in turn, is likely to generate more massive submerged structure for cover. Furthermore, detritus-based food resources are likely to be more abundant near highly productive mangroves.

Most mangrove-dominated estuaries contain examples of all these habitats and may thus provide a diversity of conditions for use by fishes.

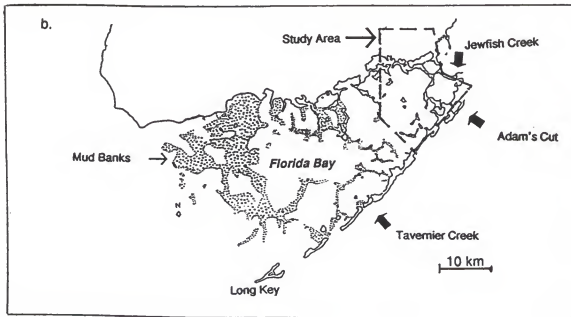
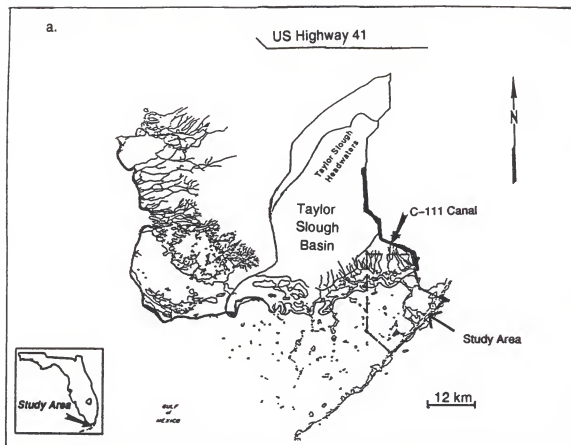
The Florida Bay Ecosystem

Florida Bay is a large (1,500 km²), mangrove/seagrass dominated estuary located in extreme south Florida. The majority of the Bay is not subject to tidal influence. Wind-driven water movements can, however, raise or lower Bay water levels rapidly. Sustained strong easterly winds can literally blow water out of Florida Bay into the open Gulf of Mexico. In similar fashion, winds from the north can accelerate the introduction of mainland drainage into the northern part of the Bay, and winds from the west can move the water into the northeastern corner of the Bay (Ginsberg 1956).

Internal circulation is restricted due to several features of the Bay. The interior contains over 300 mangrove-fringed and overwash islands. On the east, U. S. Highway 1 separates Florida Bay and Barnes Sound with only one pass and two culverts providing water exchange. On the west, it is separated from the open waters of the Gulf of Mexico by a series of mud banks that are at least 2.0 km wide and are often exposed (Holmquist et al. 1989b) (Figure 1-1). The lower Bay is separated from the thermally stable and constant flow of the Gulfstream by a series of limestone islands known as the Florida Keys. Several major passes occur through the Keys in the western Bay, but in the

Figure 1-1. Regional maps of the study area showing features of the upstream drainage basins and Florida Bay.

- a. Boundaries of drainage basins and tributaries to northeastern Florida Bay. (Source: Schomer & Drew 1982).
- b. Florida Bay showing the extensive mudbank system (stipple pattern). Arrows indicated passes to the Atlantic Ocean and Barnes Sound. (Source: Holmquist et al. 1989b)



northeastern portion, only one pass exists, a man-made cut through Key Largo to the ocean side (Adam's Cut) (Figure 1-1). On the northern boundary of the Bay are the Florida Everglades.

The Florida Bay area is subject to an annual water deficit with evaporation exceeding total rainfall (Tabb et al. 1962). Annual rainfall in northeastern Florida Bay ranges from 1600 mm on the mainland at Homestead to 1200 mm on the south at Key Largo. The climate of subtropical south Florida is characterized by a relatively long and severe dry season (November through April) and a wet season (May through October) (Schomer & Drew 1982).

Sea level becomes relatively high on an annual basis from August to December reaching a maximum of about 15 cm above the annual average in October (Ginsberg 1956, Provost 1973, Holmquist et al. 1989b). By late November or early December, Bay level recedes to the annual average, which probably accelerates the drainage of freshwater into the Bay from the mainland. At this time, the zone of reduced salinity may extend farther south and southeast into mid- and downstream Florida Bay areas.

The major source of freshwater flow into Florida Bay is from a series of approximately 20 creeks and Taylor River, which carry surface water from the Taylor Slough/C-111 drainage area into the Bay. This system is smaller than the

Shark River Slough, a separate system which extends from Lake Okeechobee southward toward the Gulf of Mexico and drains most of the Everglades.

These overall features contribute to several environmental and biological patterns. Gradients in environmental variables occur in Florida Bay, from southwest to northeast. These gradients include amount of water exchange, sediment depth, and seagrass standing crop (Zieman et al. 1989). The area northeast of the central line of mud banks is characterized by very restricted circulation and no tidal influence (Schomer & Drew 1982). A thin sediment veneer covers the basin bedrock in the northeast Bay, deepening towards the southwest. In addition, seagrass density and productivity decreases dramatically from southwest to northeast (Zeiman et al. 1989).

Problem Definition

Water management decisions in the eastern Everglades have potentially impacted Florida Bay through changes in the timing and quantity of freshwater discharge. Under pre-drained conditions, in this area, surface freshwater moved over grassy marl prairies that were seasonally flooded (Schomer & Drew 1982). A complex network of streams, bordered by mangroves and other shrubs carried freshwater inflow to receiving waters downstream in a manner that was presumably both gradual and dispersed.

Beginning in the early 1900s, construction began on an extensive system of canals and ditches throughout much of

the Everglades system. The effects of these canals may have included the overall reduction in the amount of freshwater storage in the system (T. MacVicar, South Florida Water Management District, personal communication). In addition, after Everglades drainage, drier conditions may have occurred more frequently in the prairies and sloughs, with greater contrast between wet season and dry. Overland flow of freshwater entering the downstream estuaries under these altered conditions has probably been more rapid and less spatially dispersed.

After entering upstream portions of Florida Bay, freshwater moves through extensive mangrove wetlands consisting of shallow swamp lands, creeks, ponds and bays, eventually reaching the open portions of Florida Bay. Changes in these brackish and marine receiving waters attributed to managed freshwater inflow may have included alteration of the annual salinity pattern, which led to unnatural cycles of both reduced and hypersaline conditions. Historical salinity data for Everglades waters, however, is lacking for the period prior to initiation of drainage.

Evidence of the ecological effects of drainage on the downstream estuary has been discerned from National Audubon Society studies showing declining populations of estuarine wading birds (e.g. spoonbills). Changes in hydroperiod have been hypothetically linked to a reduced fish and shellfish prey-base for the birds (National Audubon Society, unpublished data, 1989). Furthermore, recent decreases in

sportfish populations have been linked to hypersalinity stress for certain sportfish in Everglades National Park (Rutherford et al. 1989). The Everglades estuaries are also critical habitat areas for other endangered aquatic species (e.g. American crocodile) that rely on the same forage base as do birds and sportfish (SFWMD 1989).

Thus, groups concerned about these problems spurred South Florida Water Management District (SFWMD) officials to take action that would return more natural drainage patterns to the estuarine areas of the Everglades. Some of these actions have focused on the C-111 Canal/Taylor Slough watershed which includes agricultural lands in a large drainage basin east of the Park. The downstream leg of the canal runs northwest to southeast, passes under U. S. Highway 1 and continues southward outside of Florida Bay, to Barnes Sound (Figure 1-1). In low flow periods, the canal has functioned like a dike by preventing overland flow of freshwater from reaching both the downstream prairies and the approximately seven small creeks tributary to northeastern Florida Bay. In high flow conditions, water still flows through, sometimes sending slugs of freshwater into northeastern Florida Bay. Local topographic conditions tend to direct more freshwater toward U.S. Highway 1 than toward the west (Tabb et al. 1967). Thus, under these management conditions, the historic salinity regime is likely to have been altered. Changes in hydroperiod have probably resulted in more severe hypersaline conditions and

sudden salinity changes of great magnitude, especially in the eastern part of Florida Bay.

In the mid-1980s engineering alterations created several cutouts, each 20 meters wide, in the south bank of C-111 canal. The cutouts were intended to restore the more dispersed and gradual pattern of freshwater inflow to northeastern Florida Bay. Furthermore, an earthen plug was installed to block the C-111 outfall to Barnes Sound except on extreme floods when SFWMD can release water by opening it with draglines. The result of these alterations was to provide more flexible management of freshwater flow to northeastern Florida Bay. The question remaining is how to utilize this flexibility to improve ecological conditions.

Objectives

Fish and Salinity

The first study objective was to determine the extent to which species composition and abundance were influenced by salinity variability in the northeastern Florida Bay study area. Because of direct and indirect salinity influences, more variable fish abundances and distinct community differences were expected at the upstream locations over an annual cycle that included both wet and dry seasonal differences in freshwater inflow. The eastern portion of the study area was also expected to be distinctly more variable than the western portion because of the influence of the C-111 Canal.

Habitat Features

Because salinity is not the only feature of the habitat that varies along the complex environmental gradient within the study area, it was also necessary to consider other features of the fixed and moveable habitat (Browder & Moore 1981) as potentially influencing fish community structure. The second study objective was to determine important habitat features that influence the abundance and species composition of mangrove fish communities and compare these features across the salinity gradient. Fixed habitat structural features such as mangrove tree height and prop root density, environmental features such as water temperature, and fish diet and predation, were expected to influence the differences among fish assemblages across environmental gradients.

Study Area

The 250 km² study area, located in extreme northeastern Florida Bay, consists of a series of shallow bays and ponds (less than 1.0 m in depth) bordered by mangroves. The upstream portion of the area is subject to freshwater inflow from seven mangrove-lined tributaries originating in the Taylor Slough/C-111 drainage basin.

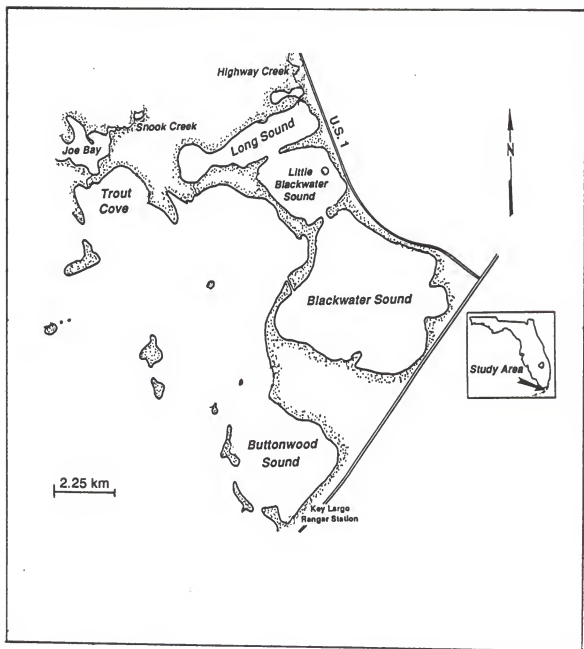
In this region of Florida Bay, rapid ecological changes can take place when salinity variations occur suddenly, as at the start of the rainy season (Montague et al. 1989). Because tidal influences are almost negligible in the northeastern Florida Bay area, salinity changes are caused

by the variations in rainfall and subsequent freshwater flowing south through the tributaries, and variations in wind speed and direction. The rate and degree of salinity change are relatively unpredictable and can be rapid (hours) or slow (days) depending on changes in the weather.

Fish Community Sampling Design

To monitor fish community changes across the dynamic salinity gradient in northeastern Florida Bay, a balanced two-way analysis of variance (ANOVA) design was used, with two systems, each composed of three salinity regimes (Figure 1-2). Generally, upstream locations included one of the creeks which carries freshwater from the Taylor Slough/C-111 Basin, an interior bay downstream from the creek but still measurably affected by freshwater inflow, and an outer bay much less affected by freshwater inflow but more by marine influences. Specifically, the locations were as follows: upstream sites were located in Highway Creek and Long Sound in the eastern system and Snook Creek and Joe Bay in the western system (Figure 1-2); midstream sites were located in Little Blackwater Sound in the eastern system and the Trout Cove area in the western system; downstream sites were located in Blackwater Sound in the eastern system and Buttonwood Sound in the western system.

Figure 1-2. Map of the Florida Bay study area.



CHAPTER 2
FISH DENSITIES AND
ASSEMBLAGE PATTERNS IN MANGROVE HABITATS:
COMPARISONS ACROSS SALINITY GRADIENTS

Fishes tolerate salinities within a range of survivability (Moyle & Cech 1988). If suitable conditions are not available within their environment, fish will experience stress, as evidenced by metabolic inefficiency and, in extreme cases, death (Moyle & Cech 1989). In general, fewer species of all faunal taxa are able to tolerate conditions in zones with salinity conditions typical of the upper estuary (Remane & Schlieper 1971). This may explain the occurrence of lower numbers of fish species that occupy such areas (Deaton & Greenberg 1986).

As an alternative strategy to permanent occupancy and metabolic adjustment, fishes can shift habitats when salinity levels generate stress (Moser & Gerry 1989). The occurrence of a salinity gradient in the estuary provides the opportunity for fish to exploit different habitats and thereby avoid unsuitable salinities by movement (Weinstein 1979). By stimulating such movements, salinity conditions may contribute to spatial and temporal fluctuations in species composition and abundances.

Contrary to what might be expected based on such physiological factors, however, abundance peaks for many estuaries occur in conjunction with the initiation of the period of maximum freshwater inflow, when salinity levels drop dramatically. Estuarine transient juveniles may constitute most of the individuals during these peak periods (Yanez-Arancibia et al. 1980, Bell et al. 1984, Pinto 1987). In some species, juvenile fishes may be capable of exploiting salinities at lower levels than adults (Gunter 1967, Moser & Gerry 1989). However, in environments with more stable salinities, estuarine transient juveniles can also be abundant (Little et al. 1988, Robertson & Duke 1990b). Thus, the role of seasonal changes in salinity on fish communities requires further exploration.

Based on investigations conducted near and within the northeastern Florida Bay study area, at the initiation of the rainy season (June), changes in salinity were expected to occur, expanding the zone of low salinity further downstream (Ginsburg 1956, Tabb et al. 1962, Lindall et al. 1973, Thayer et al. 1987). This zone of lower salinity was expected to persist after the end of the rainy season, as freshwater from the eastern Everglades gradually drained into Florida Bay.

Toward the goal of understanding the influence of freshwater inflow on fishes, the objective of this portion of the study was to identify spatial and temporal patterns in fish assemblages across the salinity gradient and thereby

test the following hypotheses. First, temporal changes in fish densities were expected to occur in conjunction with salinity changes. Secondly, in areas where salinities were more variable, numbers of species of fishes were expected to be lower than more stable areas. Thirdly, a community of fishes including estuarine transient juveniles was expected to occur in the study area. Finally, relatively lower densities were expected to occur in the upstream locations as an function of variable salinity conditions.

Materials and Methods

Pilot Study

A six-month pilot study was conducted to determine the most effective methods for quantitatively sampling fishes in mangrove prop root habitat throughout northeastern Florida Bay. Absence of tidal exchange in the study area was an important factor in selecting methods. Both collecting and observational methods were explored. Collecting gear selected for preliminary testing included minnow traps, Caribbean fish traps, gill nets, pull-up nets and enclosure nets with rotenone. The two visual census methods tested were: 1) direct recording of fishes observed with mask and snorkel on underwater data sheets and, 2) underwater video taping. Two complementary methods were selected from those tested in an attempt to sample the entire fish community. These two methods were enclosure nets and direct visual observation.

Design of the Main Study

The climate of subtropical Florida is characterized by a relatively long and severe dry season (November through April) and a wet season (May through October). Thus, the sampling schedule included monthly sampling for a one year period to encompass the influence of changes triggered by seasonal climatic conditions.

To monitor fish community changes across the dynamic salinity gradient of northeastern Florida Bay, a balanced sampling design suitable for analysis of variance was used. The design consisted of two systems, each having three locations along the salinity gradient (Figure 2-1 and Table 2-1). Based on the pilot study, this geographic design was to encompass three regimes of salinity variability within each system:

Upstream:	low mean	/	high variation;
Midstream:	mid mean	/	mid variation;
Downstream:	high mean	/	low variation.

Enclosure Nets

From the pilot study, one collecting method proved to be superior to the others, both in terms of sampling the breadth of species at the sites and providing a quantitative sample of fish density. This was the enclosure net first used by Thayer et al. (1987) to sample mangrove shoreline fishes in western and central Florida Bay. This method was selected for targeting small benthic and water column fish in particular.

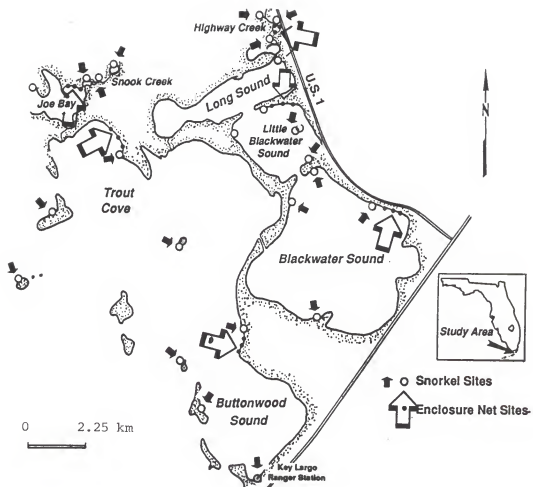


Figure 2-1. Northeastern Florida Bay study area with sampling stations indicated.

Table 2-1. List of stations used in sampling fish in mangroves using enclosure nets and visual census surveys.

System	Gradient	General Location	Enclosure Net Stations		Visual Census Stations	
			Number	Name	Number	Name
West	Upstream	Joe Bay	1	east	1	Snook Creek Pond 1
			2	mid	2	Snook Creek Pond 2
			3	west	3	Snook Creek Pond 3
	Midstream	Trout Cove	4	northeast	4	west Joe Bay*
			5	mid	5	southeast Trout Cove
			6	southeast	6	Tern Key
	Downstream	Buttonwood Sound	7	northeast	7	Deer Key*
			8	mid	8	Duck Key
			9	southwest	9	Buttonwood Point
East	Upstream	Highway Creek	10	east	10	Whaleback Key
			11	island	11	Unnamed Key
			12	west	12	Key Largo Ranger Station
			13	east	13	Shark Pond
	Midstream	Little Blackwater Sound	14	island	14	Highway Creek Big Island
			15	west	15	Critter Pond*
			16	east	16	northeast Long Sound*
			17	mid	17	northeast L. Blackwater Sd.*
	Downstream	Blackwater Sound	18	west	18	northwest L. Blackwater Sd.*
			19	mid	19	L. Blackwater Sd. island
			20	west	20	south L. Blackwater Sd.
			21	near Gilberts	21	trestle
			22	mid	22	Gilberts
			23	far	23	hydrostation
			24		24	Bush Point

* Stations that were dropped from the analysis due to missing data as a result of numerous poor visibility days primarily in 1990.

Sites. Because enclosure net stations were located in open bays, sites were selected that were protected from prevailing direct winds. Such siting prevented the wind from pulling the bottom of the net off the substrate. Sites were further chosen to have between 20 and 100 cm mean water depth at the outer prop root edge. This criterion was intended to provide some uniformity among the sites in terms of volume of water enclosed in the net. At each site, a natural berm consisting of packed detritus approximately 15 cm high and 30 cm wide occurred along the landward edge. This berm was exposed at high tide and provided a bank beyond which fish could not escape when rotenone was applied within the net (see below).

Procedures. At the start of the study, three sites were selected in each of the six general locations. A maximum of three enclosure nets could be deployed at each location by two persons in a day if the nets were deployed no more than approximately 1.0 km from each other. Environmental measurements taken during each collection included water depth, salinity, temperature, wind speed, wind direction, and air temperature. Salinity and water temperature were measured with a calibrated electronic instrument (YSI Model 33 S-C-T meter). For salinities above 35 ppt, a calibrated hand-held refractometer was used.

For each net, two 30 cm wide paths were cut perpendicular to the shoreline through the mangrove fringe back to the berm. The paths were cleared of bottom roots

and overhanging branches so that a person could walk up the path carrying one end of the 30 m long net.

The same site was sampled repeatedly throughout the study unless "stress" was observed in submerged vegetation. For example, sites with clay sediments supporting seagrasses had suffered some visible damage (e.g. grass trampling) from the sampling procedure by the fourth month at three stations. To maintain consistency in types of habitat encompassed by the nets, at these three sites, one new path was cut so that an unimpacted site could be sampled adjacent to the old one. These minor site changes were taken into account in later calculations of net area sampled.

On the day of sampling, a 6.0 mm mesh nylon seine was deployed by two people who carried it, scrolled around two wooden dowels, to the mid-point between the two prepared paths. Starting 10 m from the edge, they waded in opposite directions parallel to the edge, unrolling the net, and then walked toward the mangroves and up the paths. The dowel end was pounded into the sediment at the landward end of the path and the lead line was pressed down into the sediments all around the bottom edge. The top edge of the net was hung over several PVC poles to prevent fish from jumping over the net. All three nets were set in similar fashion (Figure 2-2).

Liquid rotenone was then applied within the enclosed area to a final concentration of 5 mg L⁻¹. Fish that immediately began to surface were collected using hand nets

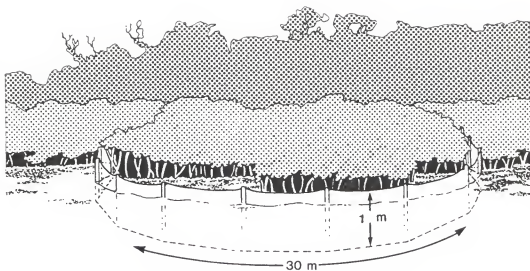


Figure 2-2. Enclosure net illustration indicating net dimensions.

for 30 to 45 minutes by two persons. After repeating the process at the other two sites, and allowing the rotenone to dissipate (approximately 3 - 4 hours), a snorkeler retrieved sunken fish and a wader collected along the berm edge from within each enclosure. Since rotenone effectiveness is reduced with decreasing temperature (Neilson & Johnson 1983), in colder months, floating fish were also collected after leaving the nets up overnight.

Fish and invertebrates collected were initially placed on ice and then frozen. Later they were identified to species and measured to total and standard (or carapace) length.

Efficiency tests. Fish recovery efficiency was tested at least once at each location using a mark-recapture method and normal net procedures. To collect test fish, several minnow traps were placed inside the area to be enclosed on the day before net deployment. After the net was in place, the minnow traps were removed, cleared and the fish placed into buckets. Fish were measured, marked by fin-clipping, and returned to the enclosed net area in minimal time. At least 30 fish were used per net in the test.

Visual Census

Based on the pilot study, direct recording of census data on underwater paper was identified as the better visual method tested. Quality of video tape was inconsistent and often low under the variable turbidity conditions encountered.

Study Sites. For visual censusing, site selection criteria included adequate depth (20 to 100 cm), red mangrove dominance, and wind-protection. At 70 m in length, however, each transect encompassed a range of depths and other physical characteristics. Four sites were randomly selected for permanent sampling stations within each of the six general locations. These sites were chosen in the same general locations as the net sites but were more widespread than the net stations (Figure 2-1).

Procedures. To prepare permanent census stations, mangrove edge transects were designated with flagging tape every 10 m along the 70 m edge. Physico-chemical variables were recorded in conjunction with each visual census (e.g. air temperature, salinity, wind conditions). Other variables measured included: 1) water depth was recorded at a permanent stake located in each transect; 2) abundance of submerged aquatic vegetation adjacent to the transects was noted using a scale of zero to three (abundant); and, 3) range of visibility was determined by using a white PVC pole set vertically into the mud and measuring the horizontal distance at which the pole became visible as one snorkeled towards it. If the visibility was less than 100 cm, the census was rescheduled. If visibility was initially poor, three attempts (on subsequent days) were made to conduct surveys. However, in some months it was impossible to conduct a visual census at particular sites.

To conduct the census, a snorkeler approached the flagged edge and remained stationary under each flag for 30 seconds, an adequate period for recording observable fish. On underwater data sheets, they recorded the species, numbers and estimated sizes of fish observed. The census surveys were conducted by myself and one assistant. Each census consisted of four complete swims of each transect.

Efficiency tests. Efficiency tests were conducted for the visual census technique using a mark-recapture method. Large fish (18-25 cm) were caught using hook and line and smaller fish (less than 18 cm) were collected with minnow traps. Tags made of plastic waterproof tape in various colors and labeled with a unique code were used. Fishing line was securely fastened to the tag and the line was sewn with a small sewing needle through the flesh just under a fish's dorsal fin (for gray snapper and larger fish) or through the lower jaw (for smaller fish).

To conduct a test, block nets were used to enclose an area of mangrove shoreline of adequate size to accommodate at least two snorkeling stations. Tagged fish (six to nine larger fish and ten smaller fish) were placed inside the enclosure for several hours to allow them to acclimatize to the habitat. Snorkelers then carefully entered the enclosed areas and conducted a visual census of the site by recording the species, tag color and code of each fish they observed. Three such tests were conducted in the summer of 1990, at three separate stations.

Definitions

As presented in Chapter 1, three categories of residency are recognized by estuarine ecologists: residents, transient juveniles, and occasional visitors. In analyzing the community in northeastern Florida Bay, several sources were consulted for life history information on individual species to designate each by residency (e.g. Odum & Heald 1972, Lee et al. 1980, Yanez-Arancibia 1980, Robins et al. 1986). Without conducting specific gonad analysis to determine maturity (e.g. Robertson & Duke 1990b), unequivocal distinction between juveniles and adults in the transient category were not possible. In addition, life history information is sketchy for all species except for certain killifish. Thus, these designations are approximate and serve for discussion purposes only. Such designations were not used in statistical analyses of the fish community.

For purposes of detailed analysis, all fish were assigned to one of three groups of species based on size, behavior and primary portion of the mangrove habitat occupied during the day. Forage fish were considered those species whose members were generally less than 15 cm in size. Two groups of forage fish occupied different portions of the mangrove habitat: benthic and water column. Benthic forage fish live in close association with the substrate and include such species as gobies, killifish and mojarras. Water column forage fish are exclusively schooling fishes, that occupy the upper water column habitats, including

anchovies and silversides. The third fish group, large roving fish, are generally greater than 15 cm in size and occupy both the bottom and water column locations. This group included such species as snook, tarpon, snappers, catfish, grunts and barracuda.

Density determinations

To obtain densities for each enclosure net sample, abundance was divided by the area the net encompassed. Areas enclosed ranged from 72 to 196 m² (mean = 119, sd = 33.2).

For visual census samples, measurements of horizontal secchi distance and fringe width were used as radii in calculating the area observed (half the area of a circle). Because it was impossible to see and accurately identify small fish at a great distance, maximum radius values of 2.0, 3.0, or 4.0 m were applied to benthic, water column and large roving fish respectively. Thus, the areas sampled in the visual censuses ranged from 1.6 and 25.0 m² at each of the eight stations along a 70 m long transect.

Analysis Methods

Temporal patterns in density. To initially inspect the data for patterns, salinity and density by fish group were graphed. Temporal patterns were examined graphically and quantitatively. For each of the three fish groups, and the three species that were most abundant within each group,

correlations were calculated between monthly averages of these fish densities and corresponding values for salinity, water temperature, and water depth.

Spatial patterns in density. To discern spatial patterns in distribution for each fish group and the top 3 species within each group, repeated measures analyses of variance (ANOVA) with multiple comparison tests were used (SAS GLM procedure). All density data was effectively normalized by log-transformation. In the initial ANOVA model, density of fish was the dependent variable and gradient position (up-, mid- and downstream) and system (east and west) were the independent variables. To explore the relative density patterns among the general locations, a second ANOVA with general location as the independent variable was conducted. Further analysis was conducted to determine if spatial variation in certain environmental parameters might indicate why the densities varied among the stations. The average values of fish density, water depth, and salinity for each station ($n = 18$ stations) were calculated. Additionally, the amount of salinity variation over time at a particular station was also calculated by determining the standard deviation of salinity. Correlations between average fish densities and the means for these parameters were then determined.

Community patterns. For comparisons among general locations, an index of species richness (Odum 1983) was calculated with total number of species as the numerator and

log-transformed abundances as the denominator. Actual fish assemblage patterns were compared to gradient positions using cluster analysis. Data for each station, date and species were used to form matrices of stations based on similarity values (SAS CLUSTER procedure). An average linkage method was used to join clusters of stations. The resulting dendrograms were compared with the gradient positions. Those stations that were placed in a group other than the correct up-, mid- or downstream position, were denoted as misclassified. A second analysis was conducted on the log-transformed densities at each station in order to more thoroughly explore the data.

Results

Tests of Recovery Efficiency

Results of recovery efficiency tests for both the enclosure net and visual census techniques measured the number of fish sampled out of the total that were at a site (Table 2-2). However, no estimate is available for either method for sample accuracy, i.e. for how many fish escaped the area as the net was being deployed or the observer approached the area.

Enclosure net efficiencies. In all tests spanning up-, mid-, and downstream locations, 492 fish were marked. Of 14 total species, 60% of the fish used in the tests were goldspotted killifish (*Floridichthys carpio*). An average of 18% of all fish were recovered in the initial dip-net collections. By adding the same-day snorkeling procedure,

Table 2-2. Efficiency test results for enclosure nets and visual census sampling obtained by mark-recapture tests.

Method	Number of Trials	Size Classes Total Length (centimeters)	Number of Fish Tagged	Mean Percent Efficiency	Standard Deviation Percent Efficiency
Enclosure net	18	2.5 to 7.5	467	36	38
	18	7.5 to 15	25	68	31
	1	15 to 25	6	100	Not applicable
Visual census	3	4 to 7	31	29	2
	3	18 to 25	22	86	12

efficiency increased by 7%. The total mean recovery rate was increased to 37% by leaving the nets up overnight and collecting the next day.

Overall, a greater percentage of larger fish were recovered than smaller (Table 2-2). Of six large fish (*Lutjanus griseus*) that were tagged, all were recovered after rotenone application. Twice as many mid-sized as small fish were recovered.

Visual census efficiencies. Individual test results for small fish (all *Floridichthys carpio*) ranged from 25 to 27% efficiency for the visual censusing method (Table 2-2). For large fish (all *Lutjanus griseus*), results ranged from 78 to 100%. Several tagged fish were observed more than one time during the four swims along the transect. Thus, when analyzing the data for each sample, to prevent counting the same fish more than once, after recording the first swim, only unique species and size classes of fish were added to the dataset for the second, third and fourth swims.

These efficiency analyses were intended to identify trends in fish recovery rates. Due to wide ranges in the test results, subsequent data analyses were not corrected for efficiencies.

Overall Abundance

Results of the visual census differed from enclosure net sampling results (Table 2-3). Enclosure net sampling resulted in the collection of 82,633 fish from 59 species and 29 families. The greatest abundance was collected at

Table 2-3. Number of fish collected using enclosure nets and observed during visual censuses. Explanation of group/residency given at end of table.

Group/ Residency	Family Species	General Locations												Total		
		Up-west		Mid-west		Down-west		Up-east		Mid-east		Down-east		Nets	Visual	
		Nets	Visual	Nets	Visual	Nets	Visual	Nets	Visual	Nets	Visual	Nets	Visual			
LR/r	Carcharhinidae (requiem shark) <i>Carcharhinus leucas</i>		2										1		1	2
LR/r	Orectolobidae (nurse shark) <i>Ginglymostoma cirratum</i>															4
LR/r	Dasyatidae (stingray) <i>Dasyatis sabina</i>															
LR/r	Elopiidae (tarpon) <i>Megalops atlanticus</i>					1		2	1						2	2
LR/r	Anguillidae (freshwater eel) <i>Anguilla rostrata</i>						6									6
WC/r	Clupeidae (herring) <i>Oplethronema oglinum</i>	3			11	1					2				1	
WC/r	<i>Clupeid (species unk)</i> <i>Harengula jaguana</i>													151	7	165
WC/r	Engraulidae (anchovy) <i>Anchoa mitchelli</i>	335	41	40										3	3	600
WC/r	<i>Anchoa cayorum</i> Ariidae (sea catfish)					2	100	454	2	17,770		4				18,605
LR/r	<i>Arius felis</i> Batrachoididae (toadfish)	4								5					5	
BF/r	<i>Opsanus beta</i> Percichthys plectrodon					1	551			2		2	3		9	554
BF/r	Gobiocidae (clingfish) <i>Gobioxys strumousus</i>	38		59		134				23		275			529	
BF/r	Bythitidae (viviparous brotula) <i>Ogilbia cayorum</i>											1			1	
BF/r	<i>Gunterichthys longipennis</i>					17									17	
	Continued					1									1	

continued

Table 2-3, continued

Group/ Residency	Family Species	General Locations									
		Up-west		Mid-west		Down-west		Up-east		Mid-east	
		Nets	Visual	Nets	Visual	Nets	Visual	Nets	Visual	Nets	Visual
LR/r	Belontiidae (needlefish)	177	53	196	407	223	478	195	95	78	219
LR/r	<i>Strongylura notata</i>					1					
BF/r	<i>Strongylura timucu</i>										
BF/r	Cyprinodontidae (killifish)										
BF/r	<i>Floeridichthys carpio</i>	1,792	676	5,011	1,294	2,183	1,095	2,127	1,473	1,056	227
BF/r	<i>Lucania parva</i>	964	2,469	924	617	1,779	1,821	1,576	3,310	389	78
BF/r	<i>Cyprinodon variegatus</i>	221	768	144	86	79	1	308	957	351	21
BF/r	<i>Fundulus grandis</i>	309	252	99	15	97	7	65	31	147	76
BF/r	<i>Fundulus confluentus</i>	98	63	91		16		47	40	199	30
BF/r	<i>Adinia xenica</i>	25				21					48
BF/r	<i>Fundulus similis</i>	2						1		10	13
BF/r	<i>Lucania godei</i>							1		1	1
BF/r	<i>Rivulus marmoratus</i>										
Poeciliidae (livebearers)											
BF/r	<i>Poecilia latipinna</i>	1,463	2,820	4,395	1,254	1,006	2,440	257	1,535	2,981	149
WC/r	<i>Gambusia</i> sp.	26	467	325	937	293	2,821	31	148	583	210
WC/r	<i>Belonesox belizanus</i>	4								2	
Atherinidae (silversides)											
WC/r	<i>Atherinomorpha stipes</i>	397	450	630	31,260	7,078	25,187		1,010	89	4,352
WC/r	Atherinidae (genus unk)										
WC/r	<i>Menidia</i> sp.	2,242	543	175	3,093	357	256	1,071	1,815	325	200
WC/r	<i>Membras martinica</i>					1					
Syngnathidae (pipefish)											
BF/r	<i>Syngnathus scovelli</i>	43	83	19		12		6		53	
BF/r	<i>Syngnathus floridae</i>	1				8				11	
BF/r	<i>Micrognathus crinitiger</i>					6				6	
BF/r	<i>Hippocampus erectus</i>					2				2	
BF/r	<i>Hippocampus zosterae</i>					1				2	
Total		959									
		1									
		13,018									
		10,237									
		1,124									
		793									
		481									
		103									
		13									
		1									
		11,000									
		1,907									
		8									
		11,042									
		120,750									
		20,690									
		9,129									
		1									
		213									
		20									
		6									
		4									
		3									

continued

Table 2-3, continued

Group/ Residency	Family Species	General Locations										Total Nets	Visual
		Up-west Nets	Visual	Mid-west Nets	Visual	Down-west Nets	Visual	Up-east Nets	Visual	Mid-east Nets	Visual	Down-east Nets	Visual
LR/O	Centropomidae (snook) <i>Centropomus undecimalis</i>	2	1			25		1		3		24	
LR/O	Echeneididae (remoras) <i>Echeneis naucrates</i>			2								1	
LR/O	Carangidae (jack) <i>Trachinotus goodii</i>											1	
LR/O	<i>Naucrates ductor</i>											2	
LR/O	Carangidae (sp unk)									1	1	4	
LR/O	<i>Caranx hippos</i>									2			
LR/O	Carangidae (juv.)	1	6							1			
LR/O	<i>Trachinotus falcatus</i>									1			
LR/O	Luftianidae (snapper)												
LR/R	<i>Luftianus focu</i>			23		12						27	
LR/R	<i>Luftianus griseus</i>	13	74	1	4,737	41	4,756	10	11	2	1,157	29	7,726
LR/R	<i>Luftianus apodus</i>	1		209		1	129				49	69	
BF/R	Gerreidae (mojarra)												
BF/R	<i>Eucinostomus</i> sp							4				13	
BF/R	<i>Eucinostomus harengulus</i>	349	32	212	128	67	446	396	135	505	458	68	882
BF/R	<i>Eugenes plumieri</i>	427	302	37	2			88	212	152		12	
BF/R	<i>Eucinostomus gula</i>	2	1	241	1,269	104	1,739	1	30	194		33	2,350
BF/R	<i>Gerres chareus</i>			7				18	3	116	143	52	900
BF/R	Haemulidae (grunts)	39				34	164						
LR/R	<i>Haemulidae</i> (sp unk)												
LR/R	<i>Haemulon parra</i>			26		102						1	
LR/R	<i>Haemulon sciurus</i>			16		1,112						11	
LR/R	Sparidae (parrotfish)											1,584	
LR/O	Lagodon rhomboides			2		20						6	
LR/O	<i>Archosargus rhomboidalis</i>					52							
LR/R	<i>Archosargus probatocephalus</i>			41		114						8	

continued

Table 2-3, continued

Group/ Residency	Family Species	General Locations								Total Nets	Visual				
		Up-west		Mid-west		Down-west		Up-east				Mid-east		Down-east	
		Nets	Visual	Nets	Visual	Nets	Visual	Nets	Visual			Nets	Visual	Nets	Visual
LR/o	Acanthuridae (surgeonfish) <i>Acanthurus chirurgus</i>									9					9
LR/o	Balistidae (leatherjackets) <i>Aluterus scriptus</i> Soleidae (sole)			1											1
BF/r	<i>Trinectes maculatus</i>	7						1			28			36	
LR/o	Tetraodontidae (puffer) <i>Sphaeroides spengleri</i>						1					1			
LR/o	Diodontidae (spiny puffer)														2
LR/o	<i>Chilomycterus schoepfi</i>							1						1	
LR/o	<i>Diodontidae (species unk)</i>			1								14			15
Total		10,824	11,185	12,723	60,275	13,712	44,703	9,547	11,301	25,115	9,280	10,912	86,212	82,833	222,960
No. Species		37	27	22	27	32	33	32	26	36	18	35	31	59	51
No. Samples		36	35	36	44	36	50	36	33	36	23	36	48	216	233

* Groups:

BF = Benthic forage fish

WC = Water column forage fish

LR = Large roving fish

/Residency: r = resident

o = occasional visitors

t = estuarine transient juvenile

ta = estuarine transient juvenile (also present as adults)

Little Blackwater Sound, the midstream-east location. The greatest number of species, however, was found in samples from Joe Bay, the upstream-west location.

Visual census sampling resulted in observation of 222,960 fish from 51 species and 31 families (Table 2-3). Greatest abundance and greatest number of species were observed in samples taken in Blackwater Sound.

Samples obtained by the two methods differed in relative abundance and numbers of species within these three fish groups (Table 2-4). For example, many more species of benthic forage fish were collected in the enclosure nets (33) than were observed in the visual census (16). In contrast, many more large roving fish species were sampled in the visual censuses (29) than in the enclosure nets (17).

Temporal Patterns in Density by Fish Group

Benthic forage fish. In Figure 2-3, one can compare changes in salinity with changes in density from the enclosure net sampling; however, no consistent patterns emerge. Great density variations occur independently of salinity changes. Salinity varied widely over the study period at the upstream/east (0.0-39.0 ppt) and upstream/west (13.0-58.0 ppt) locations. Salinity also ranged widely at the midstream/east location (19.5-50.0 ppt). However, at the other three locations (downstream/west, downstream/east and midstream/west), salinity remained high (29.8 to 54.0 ppt) throughout the study. Not only was the period of low salinity longer in the upstream/east location, but also, a

Table 2-4. Summary of abundances and number of species by method of collection and fish group.

Fish Group	Parameter	Methods	
		Enclosure Nets	Visual Census
Benthic Forage Fish	Total	45,458	39,476
	No. Species	33	16
Water Column Forage Fish	Total	35,926	156,610
	No. Species	9	6
Large Roving Fish	Total	1,249	26,874
	No. Species	17	29
All Fish	Total	82,633	222,960
	No. Species	59	51

Benthic Forage Fish Density & Salinity vs. Month

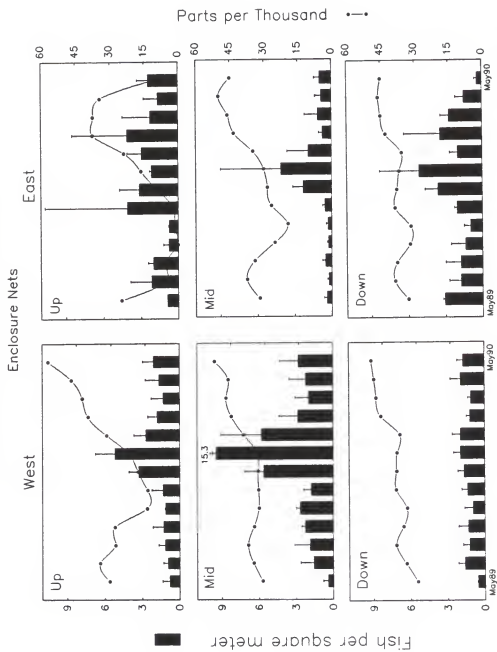


Figure 2-3. Density of benthic forage fish collected with enclosure nets in mangrove habitats (histogram) and corresponding salinity measurements (lines). Error bars indicate standard deviation among the three enclosure nets deployed in each general location.

substantial decrease (from 35.0 ppt to 10.4 ppt) was evident in June 1990, that did not occur in stations sampled in the upstream/west location (which became increasingly hypersaline).

None of these salinity changes correspond with patterns observed for fish densities. Density of benthic forage fish peaked in winter months at four of the six general locations (Figure 2-3). The highest density collection (13.6 fish m^{-2}) was at the mid-Trout Cove station in winter 1989; lowest density occurred at the mid-Little Blackwater Sound in the June 1989 (0.12 fish m^{-2}).

Water column forage fish. In Figure 2-4, one can compare changes in salinity with changes in density from the enclosure net sampling; again, however, no consistent patterns emerge. Density of water column fish was highly variable and the graphs illustrate no consistent seasonal patterns. In general, either very low or very high densities of these schooling fishes were collected. The highest density collection (25.3 fish m^{-2}) occurred at mid-Little Blackwater Sound in September 1989. No water column forage fish were collected in several samples. As with the benthic forage fish, these density fluctuations were also not related to the seasonal fluctuations in salinity.

Large roving fish. In Figure 2-5, changes in salinity can be compared with changes in density for this group from the visual census sampling; again, however, no consistent temporal patterns emerge. In the upstream/west location,

Water Column Forage Fish

Density & Salinity vs. Month

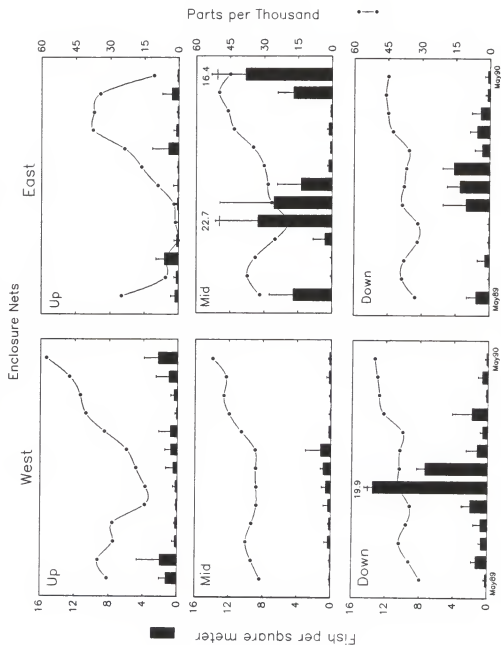


Figure 2-4. Density of water column forage fish collected with enclosure nets in mangrove habitats (histogram) and corresponding salinity measurements (lines). Error bars indicate standard deviation among the three enclosure nets deployed in each general location.

Large Roving Fish

Density & Salinity vs. Season

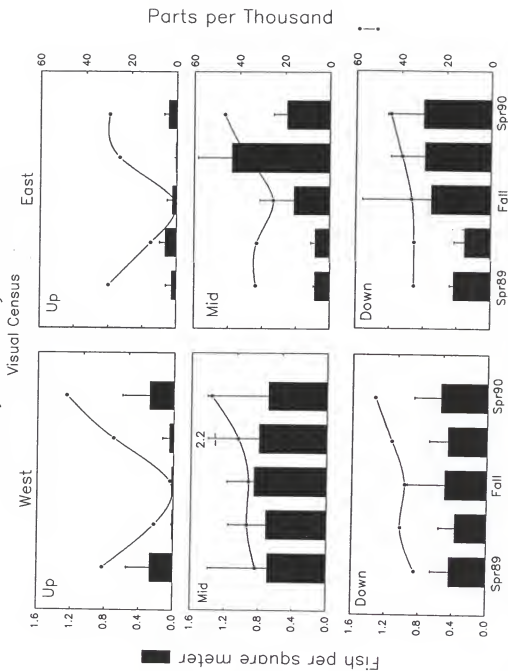


Figure 2-5. Density of large roving fish sampled by visual census in mangrove habitats (histograms) and corresponding salinity measurements (lines). Error bars indicate standard deviation among the visual censuses.

the visual census stations were notably fresher (1.4-50.0 ppt) than the corresponding net stations (13.0-58.0 ppt) (Figures 2-3 & 2-5). In this location, the visual census stations were located within the creek itself while the net stations were located in Joe Bay immediately at the creek mouth (Figure 2-1). These seemingly slight differences in location may have contributed to observed differences in salinity patterns for the visual and net stations.

For the visual census, the salinity patterns in both the eastern and western upstream locations were similar to each other except in spring 1990, when freshwater entered the upstream/east location reducing salinity to 30.0 ppt and the upstream/west location became strongly hypersaline (47.3 ppt) (Figure 2-5). The midstream/east location was overall more variable than the midstream/west location. At the mid/west and downstream visual census locations, salinity patterns were uniformly high.

Density of large roving fish ranged from zero at the uppermost upstream/west location in the spring, fall and winter of 1989, to 2.3 fish m^{-2} at Duck Key (midstream/west) in winter. From the graphs, it appears that changes in density of this group were independent of salinity changes (Figure 2-5).

Temporal correlations. No significant correlations between temporal changes in salinity or water depth, and temporal changes in fish densities were found (Table 2-5). However, changes in water temperature were correlated with

Table 2-5. Correlations between fish density for each month averaged over the stations and salinity, water temperature and water depth. Data for large roving fish were obtained by visual censuses. Data for benthic and water column forage fish were obtained with enclosure nets. All density data were converted to logarithms ($\log x + 1$) prior to calculations. Significant ($p < 0.05$) correlations are underlined.

Species or Category	Salinity		Water depth		Water Temperature	
	correlation	p-value	correlation	p-value	correlation	p-value
Benthic Forage Fish	+0.17	0.5769	+0.05	0.8721	<u>-0.80</u>	<u>0.0010</u>
Water Column Forage Fish	+0.06	0.8437	+0.57	0.4350	-0.04	0.8986
Large Roving Fish	+0.31	0.2996	-0.35	0.7145	<u>-0.76</u>	<u>0.0028</u>

density of benthic forage fish and large roving fish. In both cases, lower abundances occurred at higher water temperatures.

Spatial Patterns in Density by Fish Group

Spatial patterns in fish density varied among the fish groups (Figure 2-6). From these graphs, one can see that only the larger roving fish group seems to vary consistently along the salinity gradient, with much lower densities at the upstream locations.

Benthic forage fish analysis of variance. Results of the repeated measures ANOVA's by fish group differed among the fish groups (Tables 2-6 and 2-7). Neither gradient position nor system were important determinants of variation in densities among the stations for the benthic forage fish group (Table 2-6). Although densities tended to vary significantly from one general location to another, these variations were not systematic along the salinity gradient, as indicated by the significant interaction between gradient and system.

The mid/west general location had significantly greater densities than the other midstream location (Table 2-7, Figure 2-6). Other locations were intermediate and not significantly different from these two.

Water column forage fish analysis of variance. Again, although densities tended to vary significantly from one general location to another, these variations were not systematic along the salinity gradient, as indicated by the

Figure 2-6. Mean density of fish by general location for each fish group. Error bars illustrate the magnitude of the standard deviation in density over all the months. Samples of benthic and water column forage fish taken with enclosure nets. Large roving fish were sampled with visual methods.

Density by General Location

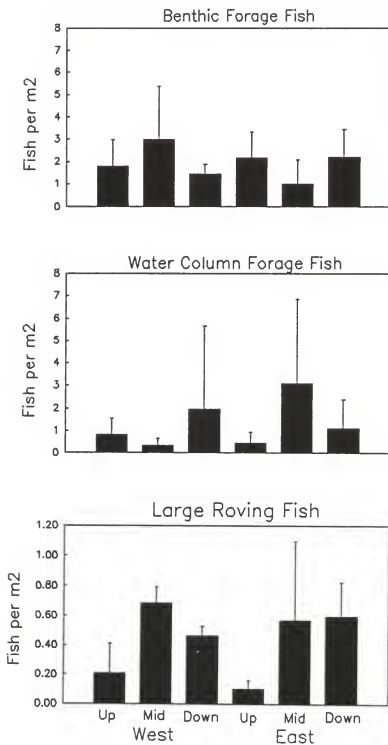


Table 2-7. Repeated measures analysis of variance with densities of fish as dependent variables and general locations as independent variables. Benthic and water column forage fish were collected using enclosure nets. Large roving fish were sampled using visual census techniques. Data were transformed to logarithms prior to performing calculations.

Source	Benthic forage fish			Water Column Forage Fish			Large Roving Fish		
	df*	F	p	df*	F	p	df*	F	p
<i>Between Stations:</i>									
Among general locations	5/12	3.77	<u>0.0277</u>	5/12	5.1	<u>0.0097</u>	5/12	2.94	0.0596
<i>Within stations</i>									
Among months	10/120	9.53	<u>0.0001</u>	10/120	5.16	<u>0.0001</u>	4/48	2.17	0.0863
Month X General locations	50/120	1.18	0.2360	50/120	4.11	<u>0.0001</u>	20/48	1.16	0.3249
Multiple comparisons among means for all months:	Location	Sign. greater than	Location	Location	Sign. greater than	Location	Location	Sign. greater than	Location
	2	>	5 (others inter-mediate)	5 & 3	>	4 & 2 (others inter-mediate)	No differences		

*Source degrees of freedom / error degrees of freedom

** General locations:

- 1 = Joe Bay, upstream/west
- 2 = Trout Cove, midstream/west
- 3 = Buttonwood Sound, downstream/west
- 4 = Highway Creek, upstream/east
- 5 = Little Blackwater Sound, midstream/east
- 6 = Blackwater Sound, downstream/east

significant interaction between gradient and system for density of water column fish (Table 2-6). Little Blackwater Sound (mid/east) and Buttonwood Sound (down/west) had significantly greater densities than Highway Creek (up/east) and Trout Cove (mid/west) (Table 2-7, Figure 2-6).

Large roving fish analysis of variance. In contrast to the other two groups, for large roving fish, a clear effect of gradient position on fish density occurred. Fish in this group were significantly less abundant at the upstream gradient locations than mid- or downstream (Table 2-6). No general locations varied significantly from the others (Table 2-7).

Spatial correlations. To analyze spatial trends, correlations between mean fish densities and salinity, salinity variation, and water depth were determined (Table 2-8). A significant correlation between average density of large roving fish and station salinity was found; lower densities occurred at stations with lower mean salinity levels and greater temporal variability. In addition, both water column forage fish and large roving fish were significantly more abundant at stations with deeper water.

Temporal Patterns in Density by Species

As indicated by the correlations between mean densities and salinity, water depth and water temperature, temporal patterns differed among the species (Table 2-9). No significant correlations were found between salinity changes from month to month and densities for any species. Temporal

Table 2-8. Correlations between fish density for each station (n=18) averaged over the months and salinity, temporal standard deviation of salinity and water depth. Density data were converted to logarithms ($\log x + 1$) prior to calculations. Significant ($p < 0.05$) correlations are underlined. Benthic and Water column forage fish were collected with enclosure nets. Large roving fish were sampled using visual techniques.

Category	Salinity		Temporal Standard Deviation of Salinity		Water Depth	
	correlation	p-value	correlation	p-value	correlation	p-value
Benthic Forage Fish	-0.08	0.7540	-0.02	0.9303	-0.12	0.6463
Water Column Forage Fish	+0.41	0.0884	-0.38	0.1233	<u>+0.48</u>	<u>0.0438</u>
Large Roving Fish	<u>+0.56</u>	<u>0.0150</u>	<u>-0.54</u>	<u>0.0208</u>	<u>+0.54</u>	<u>0.0213</u>

Table 2-9. Correlations between fish densities for each month (n=13) averaged over the stations and salinity, water temperature and water depth. Density data were converted to logarithms (log x + 1) prior to calculations. Significant ($p < 0.05$) correlations are underlined.

Species	Method	Salinity correlation p-value	Water depth correlation p-value	Water Temperature correlation p-value
<i>Floridichthys carpio</i>	Nets	+0.15	0.6117	-0.50
<i>Lucania parva</i>	Nets	-0.06	0.8420	<u>-0.69</u>
<i>Poecilia latipinna</i>	Nets	+0.49	0.0888	<u>-0.72</u>
<i>Anchoa mitchelli</i>	Nets	+0.04	0.8961	<u>0.0056</u>
<i>Menidia</i> spp.	Nets	+0.18	0.5638	+0.24
<i>Atherinomorus stipes</i>	Nets	-0.14	0.6449	+0.51
<i>Lutjanus griseus</i>	Visual	+0.47	0.1039	-0.14
<i>Strongylura notata</i>	Visual	-0.35	0.2382	<u>-0.92</u>
<i>Haemulon sciurus</i>	Visual	-0.04	0.8931	<u>0.0001</u>
			<u>0.0026</u>	<u>0.0482</u>
			<u>0.0475</u>	<u>0.0233</u>

patterns in water temperature were significantly correlated with densities of several species. *Lucania parva*, *Poecilia latipinna*, *Lutjanus griseus*, and *Strongylura notata* were less abundant when the water temperatures were higher. In contrast, greater abundances of *Haemulon sciurus* were observed in warmer months. Periods of higher water levels in the study area (e.g. late fall) corresponded to periods when greater densities of *Atherinomorus stipes*, *Strongylura notata*, and *Haemulon sciurus* were collected. In contrast, *Lucania parva* was in greater abundance during low water periods.

Spatial Patterns in Density by Species

Analyses of variance. Density patterns varied for the top three species of benthic forage fish (Figure 2-7). Results of repeated measures analyses of variance also differed among these species (Tables 2-10 and 2-11). *Poecilia latipinna* was more abundant at the midstream locations, particularly Trout Cove (mid/west). Distributions of *Floridichthys carpio* and *Lucania parva* were not significantly influenced by gradient position or system. However, *Floridichthys carpio* was more abundant at Trout Cove than all other locations and *Lucania parva* was most abundant at Blackwater Sound (mid/east).

The top three water column forage fish species differed in spatial distribution (Figure 2-8). Repeated measures ANOVA results also varied among these species (Table 2-12 and 2-13). Distribution of the silversides differed

Figure 2-7. Mean density of fish by general location for the three most abundant species in the benthic forage fish group. Error bars illustrate the magnitude of the standard deviation in density over all the months.

Density by General Location

Top 3 Benthic Forage Fish Species

Enclosure Nets

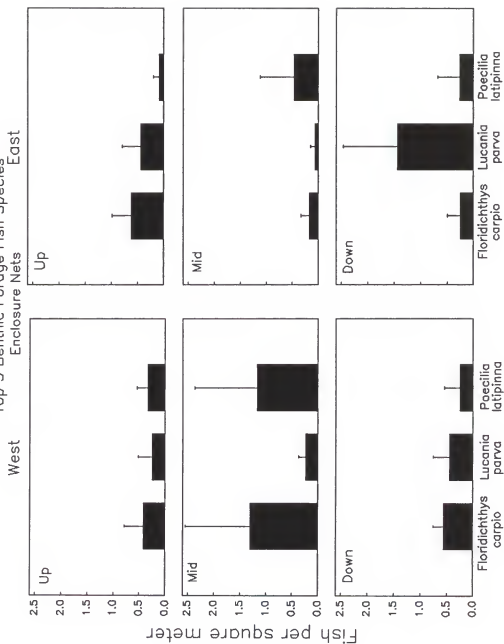


Table 2-10. Repeated measures analysis of variance with density of benthic forage fish as the dependent variable and gradient and system as the independent variables. Samples were taken within mangrove habitats using enclosure nets. Densities were transformed to logarithms prior to calculations.

Source	<i>Floridichthys carpio</i>			<i>Lucania parva</i>			<i>Poecilia latipinna</i>		
	df*	F	P	df*	F	P	df*	F	P
<i>Between Stations:</i>									
Among gradient positions	2/12	3.29	0.0726	2/12	12.96	0.0010	2/12	5.96	0.0160
Among systems	1/12	33.49	0.0001	1/12	2.23	0.1610	1/12	6.00	0.0306
Gradient X System	2/12	21.21	0.0001	2/12	5.09	0.0251	2/12	1.71	0.2229
<i>Within Stations:</i>									
Among months	10/120	7.43	0.0001	10/120	7.70	0.0001	10/120	5.73	0.0002
Month X Gradient	20/120	3.62	0.0001	20/120	1.99	0.0317	20/120	2.73	0.0002
Month X System	10/120	1.43	0.1777	10/120	1.54	0.1712	10/120	1.28	0.2827
Month X System X Gradient	20/120	2.14	0.0072	20/120	1.45	0.1561	20/120	0.93	0.5113
Multiple comparisons among means for all months:	Location	Sign. greater than	Location	Location	Sign. greater than	Location	Location	Sign. greater than	Location
Gradient positions	No differences			Down	>	Up & Mid	Mid	>	Up & down
Systems	West	>	East	No differences			West	>	East

*Source degrees of freedom / error degrees of freedom

Table 2-11. Repeated measures analysis of variance with density of benthic forage fish as the dependent variable and general location as the independent variables. Samples were taken within mangrove habitats using enclosure nets. Densities were transformed to logarithms prior to calculations.

Source	<i>Floridichthys carpio</i>			<i>Lucania parva</i>			<i>Poecilia latipinna</i>		
	df*	F	p	df*	F	p	df*	F	p
Among general locations	5/12	16.50	0.0001	5/12	7.67	0.0019	5/12	4.26	0.0184
Among months	10/120	7.43	0.0001	10/120	7.70	0.0001	10/120	5.73	0.0002
Month X general location	50/120	2.59	0.0001	50/120	1.68	0.0314	50/120	1.72	0.0426
Multiple comparisons among means for all months	General location **	Sign. gr. location than	General location **	General location **	Sign. gr. location than	General location **	General location **	Sign. gr. location than	General location **
	2	>	All	6	>	All	2	>	All
	3 & 4	>	5 & 6 (others inter-mediate)						

* source degrees of freedom / error degrees of freedom

** General locations:

1 = Joe Bay, upstream/west

2 = Trout Cove, midstream/west

3 = Buttonwood Sound, downstream/west

4 = Highway Creek, upstream/east

5 = Little Blackwater, midstream/east

6 = Blackwater Sound, downstream/east

Figure 2-8. Mean density of fish by general location for the three most abundant species in the water column forage fish group. Error bars illustrate the magnitude of the standard deviation in density over all the months.

Density by General Location

Top 3 Water Column Forage Fish Species

Enclosure Nets

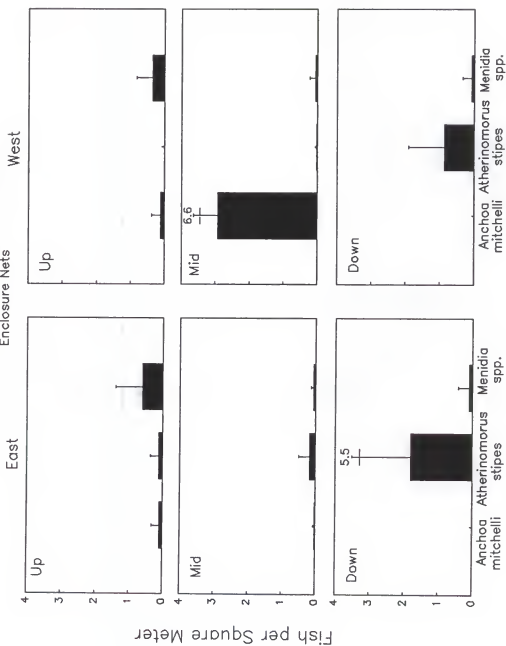


Table 2-12. Repeated measures analysis of variance with density of water column forage fish as dependent variables and gradient and system as independent variables. Samples taken within mangrove habitats using enclosure nets. Densities were transformed to logarithms prior to calculations.

Source	<i>Anchoa mitchelli</i>				<i>Atherinomorus stipes</i>				<i>Menidia spp.</i>			
	df*	F	p		df*	F	p		df*	F	p	
<i>Between Stations:</i>												
Among gradient positions	2/12	10.95	0.0020		2/12	116.61	0.0001		2/12	13.44	0.0009	
Among systems	1/12	13.41	0.0031		1/12	20.32	0.0007		1/12	1.62	0.2272	
Gradient X System	2/12	11.32	0.0017		2/12	2.81	0.1001		2/12	0.51	0.6136	
<i>Within Stations:</i>												
Among months	10/120	4.73	0.0060		10/120	8.54	0.0001		10/120	3.05	0.0065	
Month X Gradient	20/120	4.95	0.0007		20/120	5.46	0.0001		20/120	2.62	0.0033	
Month X System	10/120	4.95	0.0047		10/120	2.46	0.0389		10/120	4.44	0.0006	
Month X System X Gradient	20/120	4.43	0.0015		20/120	3.00	0.0031		20/120	2.70	0.0025	
Multiple comparisons among means for all months:	Location	Sign. greater than	Location		Location	Sign. greater than	Location		Location	Sign. greater than	Location	
Gradient positions	Mid	>	Up & down		Down	>	Up & Mid		Up	>	Mid & down	
Systems	East	>	West		West	>	East		No diffs	>	East	

*Source degrees of freedom / error degrees of freedom

Table 2-13. Repeated measures analysis of variance with density of water column forage fish as the dependent variable and general location as the independent variable. Samples were taken in mangrove habitats with enclosure nets. Density data were transformed to logarithms for calculations.

Source	<i>Menidia spp.</i>			<i>Atherinomorus stipes</i>			<i>Anchoa mitchelli</i>		
	df*	F	p	df*	F	p	df*	F	p
Among general locations	5/12	5.90	0.0056	5/12	51.83	0.0001	5/12	11.59	0.0003
Among months	10/120	3.05	0.0065	10/120	8.54	0.0001	10/120	4.73	0.0060
Month X general location	50/120	3.02	0.0001	50/120	3.68	0.0001	50/120	4.74	0.0001
Multiple comparisons among means for all months	General location **	Sign. gr. location than	General location	General location **	Sign. gr. location than	General location	General location **	Sign. gr. location than	General location
	1	>	All except 4	3	>	All	5	>	All
				6	>	All others			

* source degrees of freedom / error degrees of freedom

** General locations:

1 = Joe Bay, upstream/west

2 = Trout Cove, midstream/west

3 = Buttonwood Sound, downstream/west

4 = Highway Creek, upstream/east

5 = Little Blackwater, midstream/east

6 = Blackwater Sound, downstream/east

significantly among the gradient positions. *Atherinomorus stipes*, the hardhead silverside, was more abundant downstream; *Menidia* spp. was more abundant upstream. Individuals of both *Menidia beryllina* and *Menidia peninsulae* were collected. The distribution of these species overlaps in northeastern Florida Bay, and distinctive characters are extremely difficult to confirm (C. Gilbert, personal communication). Thus, *Menidia* spp. has been used in this study to designate these species. *Anchoa mitchelli*, although not influenced by gradient or system, was significantly more abundant at Little Blackwater Sound (mid/east) than at the other general locations.

Patterns varied in spatial distributions for the top three species of large roving fish (Figure 2-9). For these species, repeated measures ANOVA results also varied (Table 2-14 and 2-15). Among these species, *Haemulon sciurus* was never present upstream. *Lutjanus griseus* was significantly less abundant up- than mid- or downstream. In contrast, *Strongylura notata* had significantly greater densities upstream/east.

Correlations. To further analyze spatial trends for these nine species, correlations between mean densities and salinity, salinity variation, and water depth were determined and are presented in Table 2-16. Densities of *Menidia* spp. were greater at locations with lower mean salinities and greater variation. In contrast, densities of *Atherinomorus stipes* were greater at locations with higher

Figure 2-9. Mean density of fish by general location for the three most abundant species in the large roving fish group. Error bars illustrate the magnitude of the standard deviation in density over all the months.

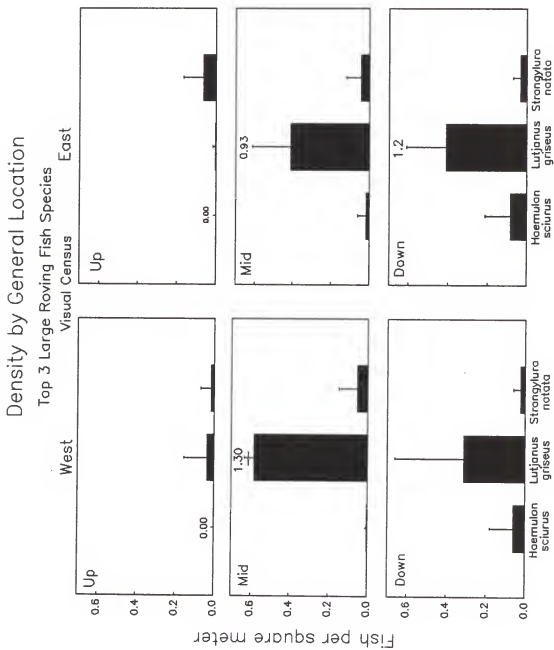


Table 2-14. Repeated measures analysis of variance with density of large roving fish as dependent variables and gradient and system as independent variables. Samples taken by visual census methods along mangrove shoreline habitats. Densities transformed to logarithms prior to calculations.

Source	<i>Haemulon sciurus</i>		<i>Lutjanus griseus</i>		<i>Strongylura notata</i>	
	df*	F	P	df*	F	P
<i>Between Stations:</i>						
Among gradient positions	2/12	2.36	0.1367	2/12	5.67	0.0185
Among systems	1/12	0.13	0.7278	1/12	0.20	0.6654
Gradient X System	2/12	0.04	0.9650	2/12	0.48	0.6317
<i>Within Stations:</i>						
Among seasons	4/48	0.29	0.8794	4/48	9.22	0.0001
Season X Gradient	8/48	0.73	0.6659	8/48	2.64	0.0309
Season X System	4/48	1.97	0.1167	4/48	2.59	0.0667
Season X System X Gradient	4/48	1.10	0.3794	4/48	1.51	0.2032
<i>Multiple comparisons among means for all seasons:</i>						
	Location	Sign. greater than	Location	Location	Sign. greater than	Location
Gradient positions	No differences		No differences	Mid & Down	>	Up
Systems	No differences		No differences	No differences		No differences

*Source degrees of freedom / error degrees of freedom

Table 2-15. Repeated measures analysis of variance with density of large roving fish as the dependent variable and general location as the independent variable. Samples were taken by visual census along mangrove shoreline habitats. Densities were transformed to logarithms prior to calculations.

Source	Haemulon sciurus		Lutjanus griseus		Strongylura notata				
	df*	F	p	df*	F	p			
Among general locations	5/12	1.03	0.4442	5/12	2.26	0.0765	5/12	3.63	0.0311
Among seasons	4/48	0.29	0.8794	4/48	9.22	0.0001	4/48	2.97	0.0416
Season X general location	20/48	1.31	0.2190	20/48	1.96	0.0480	20/48	1.51	0.1489
Multiple comparisons among means for all seasons	General Sign. General location greater location **		General Sign. General location greater location **		General Sign. General location greater location **				
General locations	No differences		No differences		4		>		1 & 3 (others interm)

* source degrees of freedom / error degrees of freedom

** general locations:

- 1 = Joe Bay, upstream/west
- 2 = Trout Cove, midstream/west
- 3 = Buttonwood Sound, downstream/west
- 4 = Highway Creek, upstream/east
- 5 = Little Blackwater, midstream/east
- 6 = Blackwater Sound, downstream/east

Table 2-16. Correlations between density for each station (n=18) averaged over all months and salinity, temporal standard deviation of salinity, and water depth. Density data were converted to logarithms ($\log x + 1$) prior to calculations. Significant ($p < 0.05$) correlations are underlined.

Species	Method	Salinity		Temporal Standard Deviation of Salinity		Water Depth	
		correlation	p-value	correlation	p-value	correlation	p-value
<i>Floridichthys carpio</i>	Nets	+0.07	0.7655	-0.12	0.6446	<u>-0.60</u>	<u>0.0079</u>
<i>Lucania parva</i>	Nets	+0.13	0.6096	-0.44	0.0665	<u>+0.62</u>	<u>0.0064</u>
<i>Poecilia latipinna</i>	Nets	+0.40	0.0935	-0.28	0.2429	-0.20	0.4165
<i>Anchoa mitchelli</i>	Nets	-0.03	0.9127	+0.14	0.5879	+0.05	0.8530
<i>Menidia</i> spp.	Nets	<u>-0.52</u>	<u>0.0253</u>	<u>+0.69</u>	<u>0.0013</u>	-0.01	0.9634
<i>Atherinomorus stipes</i>	Nets	<u>+0.60</u>	<u>0.0087</u>	<u>-0.72</u>	<u>0.0007</u>	+0.45	0.0626
<i>Lutjanus griseus</i>	Visual	<u>+0.58</u>	<u>0.0108</u>	<u>-0.58</u>	<u>0.0123</u>	<u>+0.53</u>	<u>0.0226</u>
<i>Strongylura notata</i>	Visual	-0.11	0.6595	-0.06	0.8234	+0.22	0.3765
<i>Haemulon sciurus</i>	Visual	+0.37	0.1300	-0.38	0.1226	+0.26	0.2942

mean salinities and less variation (Table 2-16). *Lutjanus griseus* also appeared to avoid the lower salinity, more variable areas. *Floridichthys carpio* was significantly more abundant at shallower stations in the study area. Species correlated with deeper waters were *Lucania parva*, *Lutjanus griseus* and possibly, *Atherinomorus stipes*.

Community Patterns

Species richness. Species richness differed among the fish groups and for all fish combined (Table 2-17). A total of 305,589 fish from 77 species was sampled using both the visual census and enclosure net methods combined. Midstream locations in both the east and west systems had the lowest species richness of the three gradient positions. Among the fish groups, benthic forage fish were also least species rich at midstream locations. Water column forage fish had distinctly lower species richness at Little Blackwater Sound, with only four species but great abundances. For large roving fish, upstream and midstream locations were lowest. For number of species alone, large roving fish species followed a clear gradient from upstream (10 and 11 species) to midstream (13 and 14 species) to downstream (20 and 22 species).

Cluster analysis. Results of two cluster analyses for species collected with enclosure nets were illustrated using dendrograms (Figure 2-10). The initial analysis classified stations based on presence of species. Most of the upstream

Table 2-17. Species richness index for fish sampled with enclosure nets and visual census. Species Richness Index = $(\text{Number of species} - 1) / \log (\text{Total individuals})$ (Odum 1983).

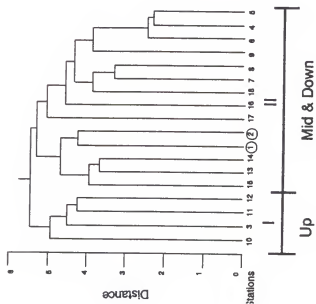
General Location	Benthic Forage Fish			Water Column Forage Fish			Large Roving Fish			All Fish		
	Total Indiv.	Number of Species	Index	Total Indiv.	Number of Species	Index	Total Indiv.	Number of Species	Index	Total Indiv.	Number of Species	Index
Up-west	15,951	24	5.5	5,408	6	1.3	450	11	3.8	21,809	64	14.5
Mid-west	16,049	14	3.1	51,052	4	0.6	5,897	15	3.7	72,998	49	9.9
Down-west	13,442	21	4.8	37,083	6	1.1	7,890	20	4.9	58,415	65	13.4
Up-east	15,716	21	4.8	4,805	6	1.4	327	10	3.6	20,848	58	13.2
Mid-east	7,434	19	4.6	25,222	7	1.4	1,739	13	3.7	34,395	54	11.7
Down-east	16,342	22	5.0	68,966	6	1.0	11,816	22	5.2	97,124	66	13.0
All	84,934	33	6.5	192,536	9	1.5	28,123	35	7.6	305,589	77	13.9

Figure 2-10. Cluster analysis dendrograms based on species collected using enclosure nets. Stations that grouped differently than actual gradient positions are designated as misclassified.

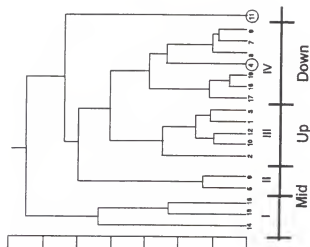
- a. Presence of each species (each species weighted equally) was used in one analysis and,
- b. Density of each species (fish per square meter) was used in the other.

Enclosure Nets

Presence



Density



⊗ = Misclassified

stations, including one in Joe Bay and all in Highway Creek, grouped separately from those located mid- and downstream. In a second analysis based on densities of each species, all but one upstream station clustered separately from the mid- and downstream locations.

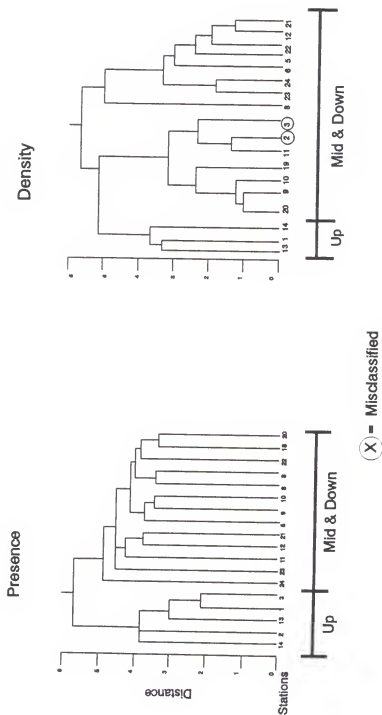
For the visual census, cluster analysis results were also graphed using dendrograms (Figure 2-11). Based on presence of species, all the upstream stations formed one cluster. Based on densities of all species, three of the five upstream stations clustered together. These were the three that were most upstream.

For each cluster group defined by the cluster analysis, the most common or dominant sets of species were identified. Three species that commonly occurred at all stations in the study area were: goldspotted killifish (*Floridichthys carpio*), rainwater killifish (*Lucania parva*), and redbfin needlefish (*Strongylura notata*). Species that were very common in upstream stations included the inland silverside (*Menidia* spp.), clown goby (*Microgobius gulosus*), tidewater mojarra (*Eucinostomus harengulus*), striped mojarra (*Eugerres plumieri*), and Mayan cichlid (*Cichlasoma urophthalmus*). Downstream species commonly included hardhead silverside (*Atherinomorus stipes*), gray snapper (*Lutjanus griseus*), silver jenny mojarra (*Eucinostomus gula*), great barracuda (*Sphyræna barracuda*), blue-striped grunt (*Haemulon sciurus*), and snook (*Centropomus undecimalis*). Midstream

Figure 2-11. Cluster analysis dendrograms based on species sampled by visual census methods. Stations that grouped differently than actual gradient positions are designated as misclassified.

- a. Presence of each species (each species weighted equally) was used in one analysis and,
- b. Density of each species (fish per square meter) was used in the other.

Visual Census



stations had mixtures of both upstream and downstream species excepting the Mayan cichlid, which was only common upstream.

Residency. Abundance and numbers of species by residency category varied among the general locations (Table 2-18). All 33 benthic forage fish species sampled were permanent estuarine residents. Among the water column forage fish, seven of the nine species observed were residents, while two (Clupeids) were occasional visitors. Large roving fish were represented in all three residency categories. Six species of large roving fish were permanent estuarine residents including needlefish, catfish, bull sharks, and stingrays. The vast majority of large roving fish were transient juveniles, however.

Frequency distribution by size varied for 6 transient species of large roving fish (Figures 2-12 and 2-13). Clearly, the mangrove habitats of northeastern Florida Bay were nurseries for *Sphyraena barracuda* most of which occurred in juvenile sizes (Figure 2-12). Snook, however, did not occur in juvenile size classes. Although adult-sized *Lutjanus griseus* appeared to share the habitat with larger-sized juveniles, since no gray snapper sampled was smaller than 7.5 cm, one can assume that young-of-the-year juveniles occur outside the mangrove habitats sampled in this study. Habitat use patterns similar to *Lutjanus griseus* were observed for *Lutjanus apodus*, *Haemulon sciurus*, and

Table 2-18. Comparison of abundance and number of species by residency, fish group, and general location. Both sampling methods were combined for the table.

Residency	Fish Group	General Locations						
		Up-west	Mid-west	Down-west	Up-east	Mid-east	Down-east	All
Residents: complete entire life cycle in the study area								
	Benthic forage fish abundance	15951	16049	13442	15712	6965	16329	84915
	Benthic forage fish species	24	14	21	21	18	22	33
	Water column forage fish abundance	4505	36460	36195	4532	23536	65843	171071
	Water column forage fish species	5	4	5	5	6	5	7
	Large roving fish abundance	236	603	1255	293	299	701	3387
	Large roving fish species	3	1	4	2	2	4	6
Transient Juveniles: juvenile offspring of species that spawn offshore								
	Benthic forage fish abundance							
	Benthic forage fish species							
	Water column forage fish abundance							
	Water column forage fish species							
	Large roving fish abundance	101	5268	6470	25	1396	9832	23092
	Large roving fish species	3	8	7	2	6	8	9
Occasional Visitors: marine and freshwater adults that occupy the study area								
	Benthic forage fish abundance							
	Benthic forage fish species							
	Water column forage fish abundance	3		1	1	2	603	610
	Water column forage fish species	1		1	1	1	1	2
	Large roving fish abundance	113	25	162	9	42	1263	1618
	Large roving fish species	5	5	9	6	5	9	19

Figure 2-12. Length-frequency histograms based on visual census data. Adult size given whenever the information was available from the literature.

- a. *Sphyraena barracuda* (great barracuda), and
- b. *Centropomus undecimalis* (snook).

Abundance by Size Class

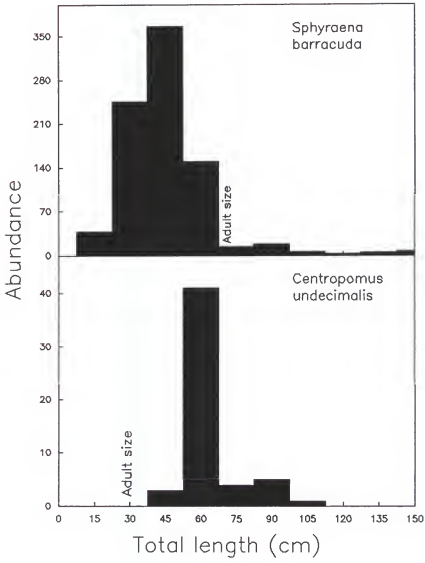
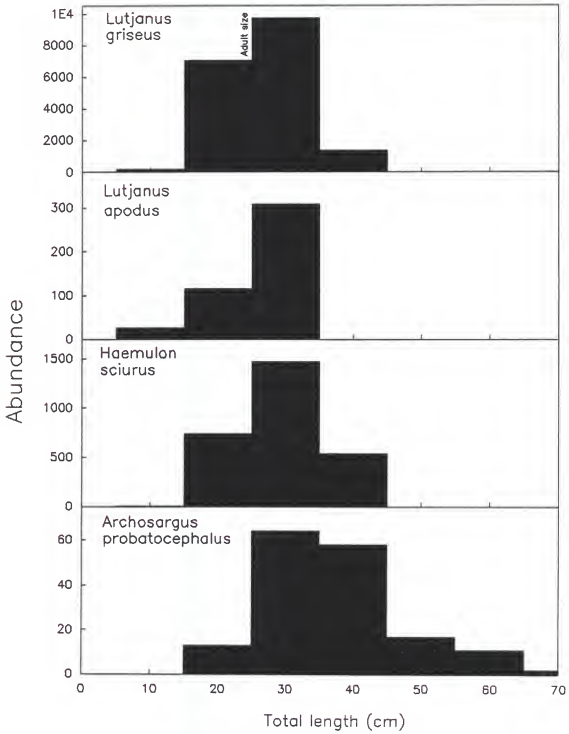


Figure 2-13. Length-frequency histograms based on visual census data. Adult size given whenever the information was available from the literature for

- a. *Lutjanus griseus* (gray snapper),
- b. *Lutjanus apodus* (schoolmaster)
- c. *Haemulon sciurus* (blue-striped grunt)
- d. *Archosargus probatocephalus* (sheepshead).

Abundance by Size Class



Archosargus probatocephalus, although adequate life history information is not available for these species to determine size at maturity (Figure 2-13).

Overall, the community was dominated by residents in both numbers of individuals (91%) and numbers of species (60%). Occasional visitors accounted for 28% of the species but less than 1.0% of the individuals. Estuarine transients (juveniles and adults) comprised 12% of the species and 8% of the abundance.

The distribution by residency varied among the locations (Figure 2-14). In terms of abundance, permanent residents dominated at all six general locations. The trend was most pronounced upstream. Transient individuals were somewhat more prevalent at mid- and downstream locations. Although less than 2.0% of the abundance, occasional visitors comprised 15 to 21% of the number of species overall.

Discussion

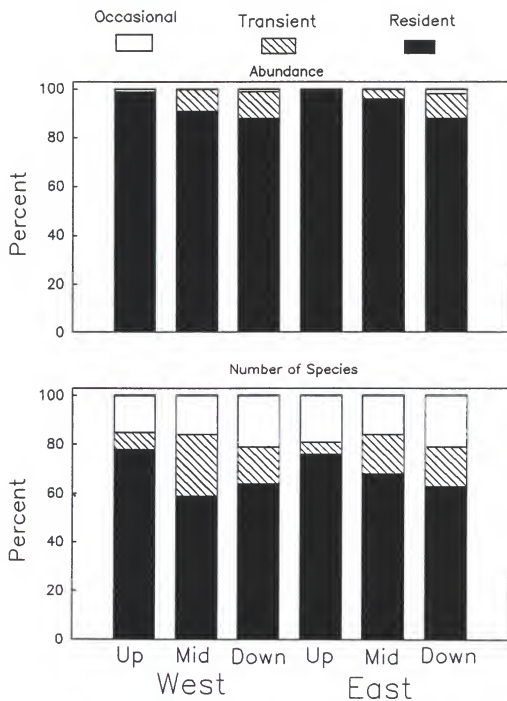
Methods

Enclosure net methodology. Using the enclosure net method, direct sampling of fish occupying submerged red mangrove shorelines was possible. The fine mesh net captured the small forage fish that numerically dominated the habitats. Inevitable escapes, especially by large roving fish, probably occurred, however, as persons deploying the net waded up to the sites. The recovery efficiencies of fishes encircled in the nets were comparable

Figure 2-14. Comparison of residency among the general locations based on percent of total abundance. Data used in calculations were taken with enclosure nets (for benthic forage fish and water column forage fish) and by visual census for large roving fish.

- a. Abundance of fish in each category.
- b. Number of species in each category.

Residency



to those found by other investigators who targeted small fish (less than about 7.0 cm in total length) in vegetated, shallow areas using (Weinstein & Davis 1980). Although rotenone required cautious handling, fish immediately began re-occupying sites after nets were removed. Rapid rotenone degradation in the relatively high temperatures which prevailed in these waters (Nielson and Johnson 1983), and dilution due to the turnover of water at the relatively open sites prevented cumulative adverse rotenone effects.

Other factors could have affected the variable efficiency of recovery from individual nets. Turbidity from disturbed sediments reduced the ability of the collectors to capture fish with dip nets. In addition, variation in winds onto the sites may have caused rotenone effectiveness to vary.

Visual census methodology. The visual census methodology had several advantages for sampling fish in mangrove habitats. The speed and flexibility of the method permitted sampling in a broad range of habitats that could not be sampled with the net, including mangrove locations with greater depths and a wider fringe. The visual method was non-destructive, thus allowing evaluation of the persistence of use by repeated observations of the same stations and fishes. The problem of net avoidance was eliminated with this method. In addition, large fish (e.g. tarpon) that would normally escape nets and trawls could be surveyed. As in studies of streams and coral reefs in which

the visual method has increasingly been used, it has possible further value for use in studies on behavior, species interactions, and microhabitat use in mangrove habitats.

Direct observational sampling also has disadvantages. Somewhat surprisingly, many fish were attracted to the snorkelers (Dibble 1991). Fishes such as snook, tarpon, gray snapper, cichlids, bluegill, and killifish, frequently came within a few inches of the snorkeler's clipboard, presumably out of curiosity. As verified in the snorkeling efficiency tests, this attraction led to double-counting of individuals on the multiple swims.

A major disadvantage of the method was its sensitivity to reduced visibility conditions. Although the fishes approached more closely in low visibility situations (1.0 to 2.0 m), the uncertainty level in identification of species was often increased. Overall, those species that tended to remain at the bottom or far back in the fringe were surveyed less accurately in deeper and low visibility sites. This problem was a particular disadvantage for surveying the benthic forage fish at deeper stations. Even in depths of only 1.0 m, the use of SCUBA equipment might be an advantage if visibility range is less than water depth since it would permit better sampling of the bottom. Some small, rare fishes and shy cryptic forms were less accurately sampled with the visual method. Finally, the occurrence of large

dangerous predators may preclude visual sampling in certain areas. Sites in deep creeks were abandoned based on sightings of large sharks and alligators.

Combined methods Using two methods to complement each other in the same habitats and regions had great advantages. The two methods increased the range of mangrove shorelines that could be surveyed. However, when using two methods, interpretation problems can arise when neither is 100% efficient. If the results do not agree, it is difficult to determine if the discrepancies are due to differences in the fish sampled or due to differences in the efficiency of the methods. In this study, the two methods targeted different size groups of fishes. Overall, benefits of using the two methods clearly out-weighed the disadvantages.

Fish and Salinity

Salinity. As confirmed in this study, salinity conditions in the area vary from year-to-year (Ginsburg 1956). The east and west systems differed greatly during the drought conditions that prevailed during the main study year. They were very similar, however, during the pilot study year when rainfall was locally more plentiful. Under low rainfall periods, the C-111 Canal may effectively block most freshwater from flowing into the western system by routing it towards the east. During high flow periods, however, when more freshwater is available for distribution, the east and west systems appear to have similar salinity patterns.

Historically, such annual differences due to local rainfall variations may have been more moderate. Before freshwater wetlands were extensively drained, freshwater probably gradually seeped into the study area from the greater Taylor Slough drainage basin, resulting in more dispersed distribution patterns and prolonged periods of lower salinity levels.

Temporal Patterns. The first hypothesis proved to be incorrect: none of the temporal patterns in density of any fish group or species examined was attributable to changes in salinity. In the study area, therefore, the fish do not seem to react to salinity changes by short-term movement in and out of the general locations (regions approximately 12 km² in area). However, patterns for all species collected were not individually analyzed. Thus, some short-term relationships may be identifiable on further examination of the data.

Temporal patterns were related to temperature, however. For benthic forage and large roving fish, as temperature increased, density decreased. Similarly, Thayer et al. (1987) and Tabb et al. (1962) also found greater densities in western and central Florida Bay in the late fall and winter when temperatures were cooler. Temporal patterns for the current study are not typical for estuarine fish populations; usually peaks occur when freshwater inflow is greatest (Gunter 1967, Weinstein 1979, Yanez-Arancibia et al. 1980, Rogers et al. 1984, Stoner 1986, Flores-Verdugo

1990). Judging from the salinity data, this would have been late summer for northeastern Florida Bay in the study year.

One possible explanation for this unusual condition may be that in the summer, high temperatures combined with low circulation to create a stressful environment for fish in the Bay (Moyle & Cech 1988). This is supported by reports by fishermen of fish kills in Florida Bay during those hot summer months (M. Robblee, Everglades National Park, personal communication).

Additionally, the density of the major component of the large roving fish group, *Lutjanus griseus*, probably accounted for much of the temperature related trend in large roving fish densities overall. The larger individuals of this species, migrate offshore in the summer, when spawning occurs, and return in the winter (Starck & Schroeder 1971, Rutherford et al. 1989). This migration may account for the reduced densities of large roving fish in the summer.

Spatial patterns. The density of fish decreases from west to east in Florida Bay (Sogard et al. 1987, 1989a). This trend appears to continue into the northeastern Bay (this study, Funicelli et al. 1986). Using an almost identical method of sampling (enclosure nets), the mean fish density found in western and central Florida Bay mangroves by Thayer et al. (1987) was 8.0 fish m^{-2} , compared to 3.3 fish m^{-2} found with nets for the northeastern Florida Bay area.

As indicated by comparisons from up- to downstream, salinity regime did not affect the overall density of benthic and water column forage fish. Furthermore, in the current study, no differences were found between the eastern and western systems. Similarly, Thayer et al. (1987) found no effect due to gradient for mangrove fishes collected with enclosure nets. The sites sampled by Thayer et al. (1987), were located in central and western Florida Bay -- from downstream near the Keys, to upstream in Whitewater Bay and Coot Bay -- and their collections were dominated by small forage fish. Thus, salinity regime may have little influence on densities of forage fish species throughout Florida Bay.

The individual species of benthic forage fish were likewise distributed widely and not systematically along the gradient. Although small benthic fishes have certain other life history characteristics that may explain the widespread distributions observed (Sogard et al. 1987), most species are notably euryhaline (Robins et al. 1986, Nordlie & Walsh 1989). Thus, they are good colonizers of all types of habitats found in Florida Bay.

In general, high variance was evident in the density estimates for water column forage fish. This was due, in large part, to their schooling behavior. With the nets, a school was either collected (and thus the abundances were great) or not collected (and thus the numbers were zero). Individual species of water column forage fish, however, do

appear to be systematically distributed along the salinity gradient. Although only one rough silverside (*Membras martinica*), was collected in the current study, they were abundant at central and western mangrove sites (Thayer et al. 1987). Abundant *Atherinomorus stipes* were collected by Thayer et al. (1987) at his most downstream locations in central Florida Bay (Crane Key and Captains Key). This corresponded to the very abundant collection of this species at the downstream-most locations in northeastern Florida Bay (Blackwater Sound and Buttonwood Sound). Since salinity regime correlated with the distribution of *Atherinomorus stipes* and *Menidia* spp., relative densities of the species in the family Atherinidae may be indicative of salinity conditions.

The density of large roving fish was dramatically lower upstream than mid- or downstream. Among the large roving fish species, however, the influence of salinity regime on spatial distributions was mixed. Blue-striped grunts and gray snapper were less abundant upstream, but redfin needlefish were more abundant at the upstream/east location than elsewhere. Thus, some species may be limited by the conditions that occur upstream, while others tend to thrive there.

Community patterns. Although no systematic pattern of distribution occurred along the gradient for benthic and water column forage fish, for the large roving fish, greater numbers of species occurred downstream. In many other

estuarine studies greater numbers of species have been found downstream (Weinstein 1979, Yanez-Arancibia 1980, Rogers et al. 1984, Sogard et al. 1987 & 1989b, Thayer & Chester 1989, Lonaragen et al. 1990). The species usually responsible for the greater downstream richness are adult members of the marine-visitor group of fishes.

Residency. Overall, the dominance over the entire study area by permanent residents (91% of abundance) was unusual even for tropical estuarine systems (Yanez-Arancibia et al. 1980, Davis 1988, Morton 1990). Only three species (13 individuals, all adults) were members of the reef community (*Acanthurus chirurgus*, *Aluterus scriptus*, *Sparisoma radians*) (Jaap 1984). The islands of the Florida Keys may inhibit connection of the fish community in Florida Bay with that of the extensive reef tract adjacent to Florida Bay (Sogard et al. 1987). The mudbanks in the central and western Bay may further inhibit travel into northeastern Florida Bay from the Gulf of Mexico. Perhaps more significantly, the moderating influence of the thermally stable Gulfstream water masses do not enter the Bay. When temperatures reach extreme low (or high) levels, those reef species that have entered Florida Bay may be forced to migrate or be killed. For example, a doctorfish (*Acanthurus chirurgus*) that was observed every month at a downstream/west station from May through December, disappeared once temperatures began to drop.

Sciaenids (drums) and bothids (flounder), major nursery species in other estuaries in the southeastern United States, Gulf of Mexico and the Caribbean (e.g. Roessler 1970, Lindall et al. 1973, Weinstein 1979, Yanez-Arancibia 1980, Stoner 1988, Sheridan 1991), were not collected at all in the present study. Since spawning takes place in the Gulf of Mexico, young juveniles may not survive the journey from distant passes into northeastern Florida Bay due to lack of tidal exchange and little circulation in the central Bay (Sogard et al. 1987).

Mangroves in northeastern Florida Bay clearly are nursery grounds, however, for several species of estuarine transients, all of which are popular sportfish: gray snapper, schoolmaster, blue-striped grunt, sheepshead and great barracuda. They also support adult snook and tarpon, species that are known to use similar mangrove habitats as nursery areas elsewhere (Gilmore et al. 1983, Seaman & Collins 1983).

A common life history pattern occurs among these fishes: recruitment from offshore as post-larvae, settlement and growth in inshore areas, and movement back offshore or to deeper water as they attain larger size classes (DeSylva 1963, Starck & Schroeder 1971, Jennings 1985, Robins et al. 1986). Since these species comprise a major portion of the large roving fish group, aspects of this basic life history pattern may indicate why they were less abundant as a group in the upstream locations.

Submerged aquatic vegetation (SAV), such as algae and seagrasses, may provide cover for newly settled forms of estuarine transient juveniles at a scale compatible with their size. As the fishes grow, however, the SAV becomes less likely to provide adequate cover for later stage juveniles, and they may seek larger forms of structure for shelter. A habitat expansion of this type was identified for juvenile gray snapper by Starck & Schroeder (1971). While smaller snappers dwell in seagrass beds, larger juvenile snappers congregate near mangroves and other brush during the day and return to feed in seagrass beds at night. The smallest gray snapper individuals found in mangroves in the current study were 7.5 cm, the same size indicated by Starck & Schroeder (1971) at which snappers expand their habitat use.

Seagrass beds are generally poorly developed in northeastern Florida Bay (Zieman et al. 1989). Abundance of SAV is temporally variable and SAV is often absent altogether upstream (Montague et al. 1988). Without SAV, young fishes may not have an adequate intermediate habitat between the planktonic and mangrove stages in which to settle. In addition, if larger juveniles (over 7.5 cm) do wander upstream, they may find inadequate food resources; many of the benthic invertebrates that they consume live epiphytically on SAV and may not occur in adequate abundance levels without SAV (Montague et al. 1989). Thus, lack of SAV may result in both reduced fish recruitment and growth

rates. This scenario may serve as an alternative or complementary hypothesis to salinity intolerance, and lack of access from distant passes, in explaining the lower overall abundances of large roving fish observed in mangrove habitats upstream.

CHAPTER 3
FISH COMMUNITIES IN
FLORIDA BAY MANGROVE SHORELINE HABITATS:
RELATIONS WITH PHYSICAL PARAMETERS AND COVER

Specific features of mangrove habitats may contribute to the structure of fish communities in predictable patterns. In the only study to specifically address this question to date, limited support for this concept was found: certain species seemed to prefer mangrove habitats to more open sites (Sheridan 1991). Other investigators have identified patterns between fish community structure and development of vegetative structure in seagrass beds (e.g. Sogard et al. 1987, Thayer & Chester 1989), kelp beds (Ebeling & Laur 1985), and littoral zone plants in ponds (Werner et al. 1983). In addition, the "rugosity" and vertical structure of coral reefs have also been identified as factors in increased densities of some species of fish (Luckhurst & Luckhurst 1978).

One role of structure in aquatic habitats is to protect vulnerable prey fishes from predators (Werner et al. 1983, Ebeling & Laur 1985). However, since food resources can become exhausted or be of lower quality in vegetated habitats, the safest refuge is not always the location that

vulnerable fishes choose (Werner et al. 1983, Schmitt & Holbrook 1985). In addition, since recruitment in aquatic systems is largely based on widely-dispersed larvae, the occupation of particular sites may be based on chance vacation of living space by a previous occupant and the largely unpredictable occurrence of available recruits from the plankton (Sale 1980, Sutherland 1980, Sale & Douglas 1984). Thus, the prediction of habitat use is a complex problem involving recruitment, species interactions, resource availability, and random influences.

If fish are not randomly distributed within the mangrove shoreline habitats of northeastern Florida Bay, it may be possible to identify features correlated with fish densities. Density can be used as a quantitative approximation of habitat quality (Sogard & Able 1991). Thus, the objective of this portion of the study was to analyze density data and habitat information in northeastern Florida Bay to determine any habitat preferences among the fish found in the mangrove shoreline.

Materials and Methods

For both the visual census and enclosure net methods, fishes and salinity were monitored at each station repeatedly over the period of May 1989, through May 1990 as described in Chapter 2. These stations were located across a gradient from upstream near sources of freshwater inflow to downstream (Chapter 2). A total of 328,960 fish

were censused or collected in enclosure nets and visual samples. Due to the nature of the sampling methods, the values for habitat structural variables were determined using slightly different procedures for the two fish data sets. Each of the 17 visual census sites analyzed consisted of 8 substations. At each substation, a transect perpendicular to the shoreline was designated. Since corresponding fish censuses were conducted at each visual census substation, all 136 substations were used in the analysis. In each of the 18 enclosure net stations, 3 transects were designated within the area repeatedly enclosed by the net. Since corresponding fish data were available for each net site as a whole, mean values for the 3 transects within each of the 18 stations were used in the analysis.

For all 190 transects, data were collected using a 1.0 m² frame. Starting at the shoreline edge, the frame was placed every three meters outward along the transect to 6 m off the mangrove fringe. The following data were collected using this overall method:

Water depth: Within each frame, four measurements were taken, one in each quadrant using a meter stick.

Fringe width: Along each transect the distance from the shoreline to the outermost mangrove fringe was measured.

Tree height: Within each frame, four measurements were taken, one in each quadrant using marked poles or by visual estimation for trees taller than 2 m.

Tree cover. The percent of canopy coverage over the frame as observed from the surface of the water was estimated.

Prop root size and density. Calipers were used to measure the diameters of red mangrove prop roots. Observations were divided into two groups: those less than and those greater than 2 cm in diameter. Numbers in each category were counted within each frame. Few prop roots less than 2 cm occurred downstream. To avoid biasing the analysis, only the data for prop roots greater than 2 cm in diameter were used.

Submerged aquatic vegetation. Within each frame, the total volume of seagrass, algae and detrital material was determined separately by placing a meter stick in each quadrant and noting the height of each component above the substrate. The percent areal coverage of each component was also estimated for each quadrant. These values were summed for the analysis.

Salinity mean: The average value for all months at each station was determined from measurements taken with a refractometer.

Salinity variation: The standard deviation for each station was calculated from the concurrent measurements.

Analysis

Datasets containing 136 visual census substations and the 18 enclosure net stations were analyzed separately. For comparison, means and standard deviations were determined for each variable. To select the most appropriate method of analysis, correlations among the variables were also calculated.

Multi-collinearity among several of the variables was revealed in the correlation analysis. Thus, principal components analysis, a multivariate technique designed to discern factors that have generated interdependence within a data set was used (Afifi & Clark 1984, Robblee 1987,

Grossman et al. 1991). Principal components of the habitat variables were calculated for both the visual census and the enclosure net data sets using the SAS correlation matrix and varimax rotation methods (Afifi & Clark 1984, Smith & Duke 1987). Each component was interpreted by examining correlations between the original variables and the derived components.

SAS FACTOR was then used to calculate individual factors from the principal components for each observation in the original data set. These uncorrelated factors were used as the independent variables in a multiple linear regression with log-transformed fish densities as the dependant variables. Fish density data were divided into 3 groups of species for the analysis based on their size, mobility and position in the mangrove habitat. These categories were benthic forage fish, water column forage fish, and large roving fish as defined in Chapter 2. All species were also analyzed separately. Only principal components with eigenvalues greater than the proportion of the variance in the data that could be explained by an individual variable (i.e. those > 1.0) were used in the regressions (Grossman et al. 1991).

The slope of the regression line describes the nature of the mangrove habitat and fish relationship. The variance in fish density explained by each component (R^2) indicates the strength of this relationship and also provides a basis

for comparisons of mangrove habitat/fish relationships between fish groups and species (Robblee 1987).

Results

Relationships Among the Habitat Variables

Correlations among habitat variables. For visual censuses and enclosure net data, mean values and correlations among the habitat variables differed (Tables 3-1 and 3-2). The visual census sites had greater water depths and tree heights but less cover than the enclosure net sites. This difference was probably due to the broader range of mangrove habitats covered in the visual census. The greatest correlation between habitat variables was found for submerged aquatic vegetation and salinity, with greater volumes occurring where salinity means were higher (Table 3-2). Salinity means were inversely correlated with salinity variation, indicating that where salinity mean was higher, salinity variation was less.

Underlying factors among habitat variables. Results of the principal components analysis and correlations of those components with each habitat variable differed for the enclosure nets (Table 3-3) and for visual the censuses (Table 3-4). The first 3 principal components explained 86.2% of the variance in the original habitat data associated with enclosure nets, and 79.7% of the variance in the enclosure net data. For both data sets, the first principal component explained 52% of the variation.

Table 3-1. Means, standard deviations, and correlations among the physical/ environmental variables associated with the 18 enclosure net stations.

	Water depth cm	Fringe width m	Tree height cm	Prop roots n	Submerged Vegetation cm ³	Salinity mean ppt	Salinity variation ppt	Tree cover %
Mean	48.53	8.88	112.49	10.82	22.30	34.10	8.87	67.02
Standard deviation	10.33	3.43	55.38	5.51	6.58	7.79	3.26	14.33
Correlations (r) between variables								
Water depth	1.000							
Fringe width	0.167	1.000						
Tree height	0.635	0.416	1.000					
Prop roots	0.285	0.633	0.606	1.000				
Submerged vegetation	0.319	0.163	0.047	-0.142	1.000			
Salinity mean	0.492	0.689	0.412	0.518	0.568	1.000		
Salinity variation	-0.417	-0.425	-0.414	-0.365	-0.599	-0.829	1.000	
Tree cover	0.732	0.393	0.735	0.572	-0.012	0.550	-0.441	1.000

Table 3-2. Means, standard deviations and correlations among the physical/ environmental variables associated with the 136 visual census stations.

	Water depth cm	Fringe width m	Tree height cm	Prop roots n	Submerged vegetation cm ³	Salinity mean ppt	Salinity variation ppt	Tree cover %
Mean	71.27	8.26	252.08	13.04	25.77	33.99	9.97	49.59
Standard deviation	20.69	4.82	102.61	11.82	10.40	8.17	5.01	12.00
Correlations (r) between variables								
Water depth	1.000							
Fringe width	0.537	1.000						
Tree height	0.391	0.435	1.000					
Prop roots	-0.187	-0.223	-0.146	1.000				
Submerged vegetation	0.632	0.599	0.472	-0.146	1.000			
Salinity mean	0.633	0.575	0.449	-0.103	0.937	1.000		
Salinity variation	-0.598	-0.530	-0.438	0.139	-0.862	-0.914	1.000	
Tree cover	0.172	0.317	0.364	-0.339	0.137	0.069	-0.032	1.000

Table 3-3. Results of the principal components analysis of the physical and environmental variables associated with the 18 enclosure net stations. Correlations greater than 0.6 are underlined.

Principal component								
	1	2	3	4	5	6	7	8
Eigenvalue	4.197	1.586	1.112	0.369	0.336	0.232	0.113	0.055
% Variance explained	52.460	19.830	13.900	4.610	4.200	2.900	1.400	0.100
Cumulative % variance explained	52.460	72.290	86.190	90.810	95.010	97.900	99.310	100.000
Correlations (r) of the original variables with the PC's								
Water depth	<u>0.931</u>	-0.151	0.029	0.192	0.080	0.248	0.066	0.021
Fringe width	0.039	-0.181	<u>0.930</u>	0.074	0.261	0.153	0.063	0.001
Tree height	0.400	-0.150	0.183	-0.008	0.263	<u>0.837</u>	0.120	0.005
Prop roots	0.145	-0.176	0.364	-0.139	<u>0.847</u>	0.262	0.101	0.021
Submerged vegetation	0.116	-0.308	0.076	<u>0.932</u>	-0.122	-0.019	-0.043	0.014
Salinity mean	0.291	-0.591	0.497	0.373	0.247	0.039	0.163	0.302
Salinity variation	-0.169	<u>0.876</u>	-0.180	-0.343	-0.139	-0.067	-0.076	0.029
Tree cover	<u>0.613</u>	-0.239	0.198	-0.121	0.241	0.338	0.583	0.029

Table 3-4. Results of the principal components analysis of the physical and environmental variables associated with the 136 visual census stations. Correlations greater than 0.6 are underlined.

Principal component								
	1	2	3	4	5	6	7	8
Eigenvalue	4.181	1.393	0.799	0.552	0.463	0.431	0.131	0.500
% Variance explained	52.300	17.400	10.000	6.900	5.800	5.400	1.600	0.600
Cumulative % variance explained	52.300	69.700	79.700	86.600	92.500	97.700	99.400	100.000
Correlations (r) of the original variables with the PC's								
Water depth	0.408	0.068	0.141	-0.082	0.201	<u>0.873</u>	-0.010	0.002
Fringe width	0.354	0.161	0.167	-0.097	<u>0.879</u>	0.198	-0.008	0.002
Tree height	0.263	0.187	<u>0.926</u>	-0.047	0.146	0.123	-0.007	0.002
Prop roots	-0.054	-0.160	-0.040	<u>0.980</u>	-0.072	-0.061	0.003	-0.001
Submerged vegetation	<u>0.896</u>	0.064	0.176	-0.051	0.221	0.218	0.167	0.186
Salinity mean	<u>0.926</u>	0.006	0.160	-0.018	0.198	0.220	0.077	-0.148
Salinity variation	- <u>0.900</u>	0.034	-0.168	0.065	-0.161	-0.194	0.306	0.008
Tree cover	-0.002	<u>0.962</u>	0.165	-0.170	0.123	0.053	0.004	0.002

Using the correlation between the original habitat variables and each component, each component was interpreted in ecological terms. Correlations greater than 0.60 were considered in the interpretation (Afifi & Clark 1984). For the enclosure net data, the first component described gradients of water depth and percent canopy cover. The second component associated with the net data described the salinity regime, in particular, salinity variation. As salinity variation increased, all other habitat variables decreased, especially submerged aquatic vegetation and tree cover. The third component was associated with fringe width. In combination, these components, describe a gradient of mangrove habitat development, together with salinity regime.

For the visual census data, the first component was most strongly correlated with salinity regime, water depth and submerged aquatic vegetation. Tree cover was the only strongly correlated variable associated with the second component, and tree height, with the third. Together with salinity regime, these components combined describe a gradient of total habitat development including both mangroves and submerged aquatic vegetation.

Relationships Between Habitat Factors and Fish Densities

The first 6 factors were included as independent variables in the multiple regression analysis. Densities of fish in the three fish groups were dependent variables (Table 3-5). No significant relationships were found for

Figure 3-5. Results of principal components regression. B, least squares regression coefficient; P, significance level; R², percent variance explained by the entire model; df, degrees of freedom; SS, sums of squares; P(R²), percent variance explained by an individual principal component.

BENTHIC FORAGE FISH (Net Data)									
Source	df	SS	P	R ²	Source	B	P	P(R ²)	Preference (p<.001)
Regression	6	2.647	0.1031	0.049	PC1	-0.057	0.0992	1.25	
Residual	209	51.601			PC2	-0.027	0.4338	0.28	
					PC3	-0.054	0.1218	1.10	
					PC4	0.065	0.0643	1.57	
					PC5	0.027	0.4382	0.27	
					PC6	-0.027	0.4409	0.27	
WATER COLUMN FORAGE FISH (Net Data)									
Source	df	SS	P	R ²	Source	B	P	P(R ²)	Preference (p<.001)
Regression	6	6.826	0.0142	0.073	PC1	0.152	0.0009	5.08	Deep water/dense canopy
Residual	209	87.084			PC2	-0.071	0.1083	1.15	
					PC3	0.040	0.3788	0.35	
					PC4	-0.017	0.7085	0.06	
					PC5	0.052	0.2525	0.58	
					PC6	0.030	0.5135	0.19	
LARGE ROVING FISH (Visual Data)									
Source	df	SS	P	R ²	Source	B	P	P(R ²)	Preference (p<.001)
Regression	6	44.100	0.0001	0.188	PC1	0.097	0.0001	6.48	High salinity/dense SAV
Residual	1617	235.130			PC2	0.032	0.0001	0.73	Dense canopy
					PC3	0.059	0.0001	2.37	Tall trees
					PC4	-0.0170	0.0410	0.21	
					PC5	0.061	0.0001	2.62	Wide fringe
					PC6	0.095	0.0001	6.31	Deep water

benthic forage fish, however (Table 3-5). As a group, these small fishes (less than 15 cm) did not appear to select habitats based on the parameters measured in this study.

A significant regression was derived for density of water column forage fish, but only the first principal component was a significant source of variation (Table 3-5). Thus, the greater mangrove canopy coverage and water depth, the greater the abundance of water column forage fish.

In contrast to the other two fish groups, for the density of large roving fish, all factors were significant sources of variation except prop root density (Table 3-5). Thus, sites with greater development of mangroves and submerged aquatic vegetation (SAV), and with higher, less variable salinity had greater densities of large roving fish.

Of the 77 total species collected, 14 had significant ($p < .0001$) regressions on the 6 factors (Table 3-6). Nine of these species were benthic forage fish and 3 were water column forage fish. The greatest amount of variation explained was 38.8%. This value was derived for densities of *Opsanus beta*, the Gulf toadfish, which was most abundant at high salinity sites with greater development of both mangrove and SAV. *Poecilia latipinna* (sailfin molly) was found most abundantly where mangrove prop roots were more dense and the width of the fringe was greater. One of the most abundant fishes, *Floridichthys carpio* (gold-spotted killifish), was more prevalent in shallow sites with more

Table 3-6. Summary of multiple regression results with 6 factors derived from the principal components analysis. Only species for which p-values were < 0.0001 are presented in the table. (Abbreviations as per Table 3-5)

Family/ species	Abundance	Adjusted R ²	Preference (p<.0001)	P(R ²)
Engraulidae (anchovies) <i>Anchoa mitchelli</i> (nets)	18,605	0.174	sparse SAV	13.7
Batrachoididae (toadfish) <i>Opsanus beta</i> (nets)	529	0.388	deep water/ dense canopy	9.0
			high salinity	14.9
			abundant SAV	8.6
			tall mangroves	4.5
Cyprinodontidae (killifish) <i>Floridichthys carpio</i> (nets)	13,018	0.278	shallow water/ open canopy	15.6
			short mangroves	7.8
<i>Lucania parva</i> (nets)	10,237	0.350	deep water/ dense canopy	10.6
			high salinity	4.9
			narrow fringe	8.3
			abundant SAV	5.5
			tall mangroves	5.2
Poeciliidae (livebearers) <i>Poecilia latipinna</i> (nets)	11,000	0.156	wide fringe	4.9
			dense prop roots	5.3
<i>Gambusia</i> sp. (nets)	1,907	0.171	high salinity	9.9
Atherinidae (silversides) <i>Atherinomorus stipes</i> (nets)	11,042	0.211	high salinity	7.7
			abundant SAV	9.2
<i>Menidia</i> sp. (nets)	4,348	0.159	low salinity	12.9
Lutjanidae (snappers) <i>Lutjanus griseus</i> (nets)	18,461	0.161	high salinity/ abundant SAV	5.3
			tall mangroves	1.0
			wide fringe	4.6
			deep water	4.4
Gerreidae (mojarra) <i>Eugerres plumieri</i> (nets)	704	0.171	low salinity	14.8
Haemulidae (grunts) <i>Haemulon sciurus</i> (nets)	2,768	0.103	high salinity/ abundant SAV	1.6
			tall mangroves	3.7
			deep water	4.8
Gobiidae (gobies) <i>Gobiosoma robustum</i> (nets)	534	0.137	low salinity	10.6
<i>Lophogobius cyprinoides</i> (nets)	200	0.321	low salinity	25.7
<i>Microgobius gulosus</i> (nets)	2,997	0.335	low salinity	19.9
			narrow fringe	11.3

open mangrove tree canopy cover. *Anchoa mitchelli* was also more abundant in open locations that were low in volume of SAV.

For several species, salinity appeared to over-ride all other variables in importance. Salinity accounted for over 10% of the variation in *Gambusia* sp. densities; this species appeared to prefer higher salinity sites in the study area. Salinity also explained from 10 to 25% of the variation in densities of *Menidia* spp., *Eugerres plumieri*, *Gobiosoma robustum*, *Lophogobius cyprinoides*, and *Microgobius gulosus*; these species were more abundant where salinities were lower. Of all the variables, salinity was a significant source of variation for 11 of the 14 species (Table 3-7). None of the other variables came close to this level of apparent importance.

Seven benthic forage fish species that were abundantly collected were not significantly correlated with the factors. Among these were the 2 *Fundulus* species and *Cyprinodon variegatus* as well as the 3 most abundant mojarras: *Eucinostomus gula*, *Eucinostomus harengulus*, and *Gerres cinereus*. These species are probably very flexible in habitat selection.

Among the species of large roving fish in the study, only the densities of gray snappers and blue-striped grunts were significantly correlated with the variables measured.

Table 3-7. Summary of the qualitative influence of the original variables on density of fish by group and species. If the value of the given variable is increased, density will either increase (+), decrease (-), or there will be no effect (0).

Category/ Species	Tree height	SAV	Water depth	Prop roots	Tree cover	Salinity mean	Salinity variation	Fringe width	Percent correlates
Benthic forage	0	0	0	0	0	0	0	0	0
Water column forage	0	0	+	0	+	0	0	0	25
Large roving	+	+	0	0	+	+	-	+	75
<i>Floridichthys carpio</i>	0	0	-	0	-	0	0	0	25
<i>Lucania parva</i>	+	+	+	0	+	+	-	-	88
<i>Poecilia latipinna</i>	0	0	0	+	0	0	0	+	25
<i>Gambusia sp.</i>	+	0	0	0	0	+	-	0	38
<i>Eugerres plumieri</i>	0	0	0	0	0	-	+	0	25
<i>Gobiosoma robustum</i>	0	0	0	0	0	-	+	0	25
<i>Lophogobius cyprinoides</i>	0	0	0	0	0	-	+	0	25
<i>Microgobius gulosus</i>	0	0	0	0	0	-	+	-	38
<i>Opsanus beta</i>	+	+	+	0	+	+	-	0	75
<i>Anchoa mitchelli</i>	0	-	0	0	0	0	0	0	13
<i>Atherinomorus stipes</i>	0	+	0	0	0	+	-	0	38
<i>Menidia sp.</i>	0	0	0	0	0	-	+	0	25
<i>Lutjanus griseus</i>	+	+	+	0	0	+	-	+	75
<i>Haemulon sciurus</i>	+	0	+	0	0	+	-	0	50
Trends among species:									
% plus	35	29	29	6	24	41	29	18	
% minus	0	6	6	0	6	29	41	12	
% zeros	65	65	65	94	71	29	29	71	

Densities of other abundant species such as *Arius felis*, *Mugil cephalus*, *Sphyræna barracuda* and *Strongylura notata* were not correlated with any of the measured variables.

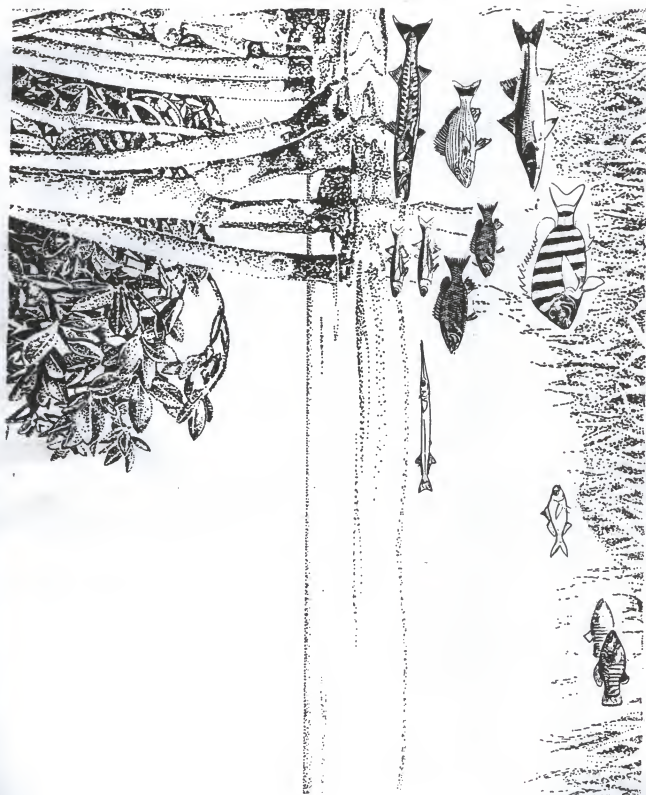
For the regressions with individual groups of fish and species, the range of percent of variance explained by the combination of variables was low overall (10.3 to 38.8%). However, the regressions were significant for 18% of all the species, and approximately one-half of the species that were collected in great abundances (i.e. over 100 individuals).

Discussion

Sites with a combination of lower mean salinity and high salinity variation had lower levels of all the other habitat development variables indicating reduced habitat development at such locations. This finding is consistent with previous results for benthic community development in northeastern Florida Bay (Montague et al. 1989).

An example of a well-developed mangrove shoreline is illustrated in Figure 3-1. In variable salinity conditions, such mangrove habitats are less likely to occur. Among the species preferring sites with greater mangrove habitat development are the snappers, grunts, toadfish, rainwater killifish, and sailfin mollies. Other species may utilize mangrove habitats on a less discriminating basis and tend to occupy all mangrove habitats. Such species include snook, barracuda and sheepshead. This assemblage of fishes is enhanced when mangrove shorelines occur and especially where

Figure 3-1. Illustration of a well-developed mangrove habitat in northeastern Florida Bay.



such habitats are well-developed. Activities which directly destroy mangrove shorelines or degrade the quality of such habitats have negative consequences for these important species of sport fish.

Although no significant relationship was found among the habitat variables and benthic forage fish as a whole, certain species did appear to discriminate on the basis of the measured variables. *Lucania parva*, *Opsanus beta*, and *Poecilia latipinna*, three abundant species collected, appeared to select sites with greater mangrove development. In contrast, *Floridichthys carpio* chose more open sites. This killifish seemed to prefer shallower locations, a trend also noted for individuals living in seagrass habitats (Sogard et al. 1987). In addition, *Opsanus beta* and *Lucania parva*, chose sites with more abundant SAV. Similarly, Sogard et al. (1987) collected greater abundances of these species in seagrass bed sites with greater vegetation densities.

In the current study, densities of water column forage fish as a group were greatest where water depths were greater and mangrove canopy more completely blocked the daylight from reaching the submerged habitat. These species use schooling as a possible defense mechanism against predators. Thus, they may use greater volumes of water to increase school size and prefer sites shaded by mangrove tree canopy for additional cover.

While these factors were important for the water column forage fish group as a whole, other features of the habitat seemed to segregate the individual species. The most abundant species in this group, *Anchoa mitchelli*, was less abundant at sites with greater volumes of SAV. This species was extremely dense at only one location in the study area (Little Blackwater Sound). Although not a variable included in this analysis, turbidity may have been the more attractive habitat feature for the bay anchovy at this site.

Of all the significant regressions for the abundant species, the range of percentage variation in fish density explained by habitat variables in this study (10.3-38.8%) was only slightly lower than that found by Sogard et al. (1987) in seagrass beds (24.8-42.7%). Thus, fish may select particular habitats based on salinity and physical features in Florida Bay but other factors (e.g. foraging requirements, species interactions) are also undoubtedly important.

The present findings do not differ greatly from long-term observations of fishes on small patches of coral, in which habitat attributes other than overall size were of little value in predicting the structure of fish assemblages (Sale & Douglas 1984). Many species of reef fish may therefore select habitats based on overall parameters (i.e. large coral reefs vs. very small patches) and not detailed features. The low magnitude of variance explained by the habitat variables measured in seagrass beds and mangroves

may be due to the selection of habitats based on general features (i.e. mangrove over seagrass habitats).

Although density of large roving fishes as a group were correlated with the physical features, some species that were categorized as "roving" in the current study may not actually roam among the mangrove habitats. Individuals of these species appear to persist at particular locations for long periods of time (based on limited observations of tagged fish). Thus, while some large fishes (such as mullet, catfish, barracuda and needlefish) may truly be wanderers and display no discrimination among mangrove shoreline habitats, other species (gray snapper and blue-striped grunts) may maintain more permanent residency at certain locations and display definite habitat preferences.

CHAPTER 4
FOOD HABITS OF MANGROVE FISHES:
A COMPARISON ACROSS SALINITY GRADIENTS

Diets have been studied for fishes associated with whole estuaries (Darnell 1961), mangroves (Odum 1971, Beumer 1978, Salini et al. 1990), salt marshes (Harrington & Harrington 1961, Rozas & LaSalle 1990), seagrass beds (Livingston 1982), lakes (Werner & Hall 1983), and streams (McNeely 1987). One successful dietary strategy identified in extremely variable habitats is omnivory, or the consumption of a wide variety of prey organisms including both plant and animal material (Darnell 1961, Harrington & Harrington 1961). Opportunism, or an ability to exploit alternative foods depending on availability, is also a valuable dietary strategy for survival in variable environments (Odum & Heald 1972, Livingston 1982, Salini et al. 1990). Trophic systems in aquatic habitats are often characterized by shared common resources among the various species of fishes (Harrington & Harrington 1961, Livingston 1982).

In estuaries, seasonality of freshwater inflow increases habitat variability upstream relative to more

stable downstream locations (Rogers et al. 1984, Moyle & Cech 1988). In northeastern Florida Bay, biomass of submerged aquatic vegetation is much lower and highly variable upstream than down (Montague et al. 1989). Abundances of polychaetes, crustaceans and other benthic invertebrates are highly correlated with plant biomass in this area: 80% of the epifauna live among the blades of seagrass and algae. For estuarine fishes, these animals are among the more heavily exploited food items (Darnell 1961, Livingston 1982).

In light of these conditions, fish diets are likely to display patterns along the gradient of salinity variation in the northeastern Florida Bay study area, due to fish foraging habits and variation in prey base. Seasonal variations in diets may also be expected. Toward the overall goal of identifying the influence of variation in freshwater inflow on habitat use, the objective of this chapter is to identify dietary components and make comparisons among the more ubiquitous and abundant species. Breadth and variability of diets should reflect environmental conditions in the more variable versus stable habitats, and over the seasons.

Materials and Methods

Fish were collected in mangrove shorelines located up-, mid- and downstream in two systems (east and west) in northeastern Florida Bay (Chapter 2). Species were selected for the analysis of food habits because they ranged across

the entire area and occurred consistently over the study period. For *Lutjanus griseus*, *Sphyræna barracuda* and *Fundulus grandis*, all samples collected were analyzed. Due to great abundances, for *Floridichthys carpio*, *Strongylura notata* and *Eucinostomus harengulus*, smallest individuals (< 3 cm) were eliminated and subsamples were selected from the remainder. Fish were not divided into size or age classes for this analysis, however.

Gut analysis of the 6 selected species was contracted out to Mote Marine Laboratory. For the laboratory analysis, 36 taxonomic levels (e.g. family) were selected for consistency with other estuarine studies of fish food habits (Brook 1977, Beumer 1978, Livingston 1982). The analysis chosen follows the "points method" of Hynes (1950). For each fish (n= 1,222), total length was recorded and the stomach was extracted. In order to identify variability among individuals, no stomachs were pooled. The material found in each stomach was distributed to a standardized level within a gridded petri dish (Hellowell & Abel 1971). Each stomach containing food was considered to be uniformly full (Starck & Schroeder 1971). Using a dissecting microscope, percent composition of each food category for each specimen was calculated by estimating the area covered by the material on the grid (Neilson & Johnson 1983).

Analysis

To determine frequency of occurrence, the number of fish in which each food item occurred was listed as a

percent of the total number of fish examined (Hynes 1950). In addition, the mean percent composition for each item was calculated by obtaining an average value for all specimens of a species. The results of both analyses are presented to give a complete picture of the relative dietary importance of the items consumed (Hyslop 1980).

Two sets of multivariate analyses of variance (MANOVA) were performed for each species with the major items found in the gut as dependent variables. All data were transformed using an arcsine square-root function prior to these calculations (Kleinbaum & Kupper 1978). The first set of MANOVAs addressed spatial variation. Gradient (upstream, midstream, downstream), system (east, west) and interaction of gradient and system, were used as independent variables. The second MANOVA looked at temporal variation. Season was the independent variable. Only major food items, defined as those which occurred in at least 20% of the specimens or exceeded an average of 4% in composition, were included in the MANOVAs.

Results

Shared Resources

Of the 24 items (counting fish as one and excluding unrecognizable), 8 occurred in all 6 species (Table 4-1). Of these, amphipods were the most ubiquitously consumed, present in at least 5% of the specimens of all species.

Table 4-1. Food items found in the stomachs of fish. Data include: % Comp, the mean % composition; % Freq, the % of specimens in which the given items occurred.

Food Items	Species	<i>Eucinostomus</i> <i>harengulus</i>	<i>Floridichthys</i> <i>carpio</i>	<i>Finchulus</i> <i>grandis</i>	<i>Lutjanus</i> <i>griseus</i>	<i>Sphyræna</i> <i>barracuda</i>	<i>Strongylura</i> <i>notata</i>	Average	
		% Comp.	% Freq	% Comp.	% Freq	% Comp.	% Freq	% Comp.	% Freq
Crustaceans									
Amphipods		25.2	76.2	47.6	27.0	4.0	19.5	2.0	7.8
Cladocerans		0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Copepods		0.9	14.4	1.2	29.9	0.8	0.0	0.0	0.0
Crabs		0.3	1.1	0.0	0.8	0.0	0.0	0.1	0.0
Isopods		2.1	12.2	2.8	6.5	12.8	23.4	1.4	3.1
Myxids		0.0	0.0	8.6	21.0	7.3	27.3	5.4	1.6
Ostracods		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cetaceans		0.2	13.8	1.2	30.8	0.0	0.0	0.0	0.0
Shrimp		0.2	2.8	2.6	6.5	4.4	19.5	4.5	3.1
Non-chitinous invertebrates									
Holothuridae		0.2	0.6	0.0	0.0	0.0	0.0	0.0	0.0
Nematodes		0.2	12.2	0.7	8.9	0.1	7.8	0.0	4.7
Nudibranchs		0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Polychaetes		1.9	18.8	0.5	6.3	0.3	2.4	1.3	7.8
Spionculids		0.0	0.0	0.0	0.0	0.9	1.3	0.0	0.0
Eggs		0.2	3.3	13.5	13.3	0.0	6.5	0.3	7.8
Fish									
Clupeidae		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Engraulidae		0.0	0.0	0.1	0.4	0.0	0.0	1.6	0.0
Belontiidae		0.0	0.0	0.0	0.0	0.0	0.0	1.0	6.3
Cyprinodontidae		0.0	0.0	0.0	1.2	1.0	1.3	2.4	26.6
Atherinidae		0.0	0.6	0.0	0.0	4.5	6.5	2.0	4.7
Synbranchiidae		0.0	0.0	0.0	0.0	0.9	2.6	0.0	0.0
Gerridae		0.0	0.0	0.0	0.0	0.0	0.0	0.1	1.6
Eleutherozoa		0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Gobiidae		0.0	0.0	0.0	0.0	0.0	0.0	0.6	1.6
Unidentified fish		0.1	2.8	0.0	0.0	0.0	0.0	8.9	48.4
Insects									
Ants		0.0	0.0	1.4	2.4	0.0	0.0	4.4	0.0
Insect larvae		0.9	6.6	0.2	0.3	1.9	0.8	0.0	0.0
Terrestrial adult insects		0.8	4.4	0.0	3.6	4.8	19.8	2.9	3.1
Mollusks									
Blivales		0.1	2.2	0.6	9.3	0.1	2.6	0.0	0.0
Gastropods		0.8	2.2	0.5	9.6	0.1	0.0	0.0	0.0
Veliger larvae		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Plants									
Algae		6.3	65.8	7.1	67.4	2.5	20.6	0.1	7.8
Seeds		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Protists									
Filamentaria		0.2	15.5	0.9	45.8	0.0	1.3	0.0	0.0
Unrecognizable		50.4	84.0	88.4	92.8	37.2	76.5	14.5	46.2
Empty		-	9.4	5.7	12.5	-	14.3	-	28.1
Total fish analyzed		181	334	248	77	64	318	64	318
Total # of items (fish=1, unrec=0)		18	20	17	13	10	17	10	17
Sizes of fish analyzed (min-max,cm)		1.1 to 13.2	3.0 to 7.7	4.2 to 13.8	12.5 to 37.7	8.0 to 50.5	9.5 to 42.0	8.0 to 50.5	9.5 to 42.0

Other items exploited to varying degrees by all 6 species included isopods, shrimp, nematodes, eggs, fish parts, adult terrestrial insects and algae.

Breadth of Diets

Excluding unidentifiable material and counting all prey fish as a single food item, of the 6 species, *Floridichthys carpio* and *Eucinostomus harengulus* foraged on the widest variety of items (20 and 18 out of 24 total, respectively) (Table 4-1). Only 2 items, however, were consumed in mean quantities exceeding 4% of total diet: amphipods and algae. Thus, although a wide variety of items were utilized by these species, a degree of specialization was apparent.

In contrast, *Fundulus grandis*, *Lutjanus griseus*, and *Strongylura notata*, not only consumed a wide range of items overall, but several items (5, 6 & 4 respectively) were consumed in mean quantities exceeding 4%. Isopods and fish were major items commonly found in all 3 of these omnivorous species.

Sphyræna barracuda was the most specialized of the species analyzed, consuming mostly fish. For this species, the benthic forage fishes in the family Cyprinodontidae were consumed with particular frequency, even though the most abundant fishes in the study area were Engraulids and Atherinids (Chapter 2).

Thus, in the study area, among the 6 species, 3 feeding strategies were evident. In one strategy, used by *Floridichthys carpio* and *Eucinostomus harengulus*, many items

were consumed, but only 2 in great abundance. In a second strategy, used by *Fundulus grandis*, *Lutjanus griseus*, *Strongylura notata*, many items were also consumed, with several (4 to 6) items ingested in substantial abundances. In the third strategy, used by *Sphyraena barracuda*, fewer items were consumed overall, with only one in significant quantity.

Diet Variability

The MANOVA results for all species, as presented in Table 4-2, indicate the degree to which location (i.e. gradient, system) was a significant source of variation in fish diets. For *Floridichthys carpio* and *Eucinostomus harengulus*, gradient position was a significant source of variation. In both species, more animal food (i.e. copepods, ostracods, nematodes) was obtained downstream than up- and midstream, while more algae was consumed upstream. The only other influence of gradient occurred for *Lutjanus griseus*, which consumed significantly more crabs upstream than mid- or downstream. For *Strongylura notata*, *Fundulus grandis* and *Sphyraena barracuda*, diets differed among the locations, but not systematically along the salinity variation gradient.

Seasonal influences on the fish diets are indicated by the second MANOVA results presented in Table 4-3. For *Floridichthys carpio* and *Eucinostomus harengulus*, algae was more important in the spring. For *Lutjanus griseus*, crabs, an important dietary item, were found abundantly in diets

Table 4-2. Comparison of food habits among gradient positions and systems. Data used are percent composition of stomach contents transformed using an arcsin square-root function. MANOVA was used to test the hypothesis that gradient and system were significant sources of diet variation. Specific F-tests to contrast means for each pair of gradient positions were used to make multiple comparisons.

Species	Independ. variable	Manova results (Wilks' lambda)		Dependent variables	Univariate results			Contrast summary**
		F-value	p-value		F-value	p-value	df*	
<i>Floridichthys carpio</i>	gradient system	7.72	0.0001	amphipods	5.59	0.0001	5/317	down > up & mid
	gradient*system	2.52	0.0261	copepods	9.06	0.0001	5/317	down > up & mid
		6.73	0.0001	ostracoda	10.01	0.0001	5/317	down > up & mid
				nematodes	4.37	0.0007	5/317	down > up & mid
<i>Eucinostomus harengulike</i>	gradient system	6.59	0.0001	forams	2.43	0.0352	5/317	up > mid & down
	gradient*system	6.00	0.0030	algae	14.41	0.0001	5/317	up > mid & down
		1.81	0.1263					
					5.88	0.0001	5/169	down > up & mid
<i>Fundulus grandis</i>	gradient system	1.12	0.3473	amphipods	4.61	0.0006	5/169	up > mid & down
	gradient*system	0.54	0.7462	isopods				
		1.62	0.1292	fish (unidentified)	1.84	0.1054	5/243	
				insects (terrestrial adults)	1.71	0.1328	5/243	
<i>Lutjanus griseus</i>	gradient system	4.93	0.0001	algae	1.84	0.1054	5/243	
	gradient*system	0.70	0.6473	crabs	1.71	0.1328	5/243	
		1.65	0.0859	isopods	0.86	0.3522	5/243	
				amtrimp	0.72	0.6122	5/243	
<i>Strongylura notata</i>	gradient system	0.58	0.5657	amphipods	3.09	0.0139	5/76	up > mid & down
	gradient*system	1.08	0.1241	isopods	15.29	0.0001	5/76	
		1.76	0.0510	amtrimp	1.34	0.2568	5/76	
				fish (unidentified)	0.91	0.4806	5/76	
<i>Sphyræna barracuda</i>	gradient system	0.58	0.5657	algae	2.39	0.0465	5/76	
	gradient*system	1.08	0.1241	amphipods	1.51	0.1868	5/310	
		1.76	0.0510	isopods	1.95	0.0859	5/310	
				amtrimp	2.75	0.0189	5/310	
<i>Sphyræna barracuda</i>	gradient system	1.06	0.3950	amphipods	0.27	0.9900	5/310	
	gradient*system	1.35	0.2578	eggs	1.62	0.1548	5/310	
		2.07	0.0325	Cyprinodontids	0.71	0.6153	5/310	
				fish (unidentified)	1.23	0.3062	5/58	
					1.24	0.3011	5/58	
					3.97	0.0036	5/58	
					0.55	0.7373	5/58	
					1.17	0.3367	5/58	

* Model degrees of freedom / error degrees of freedom

** If no contrast is indicated, either an interaction or no significant differences occurred.

Table 4-3. Comparison of food habits among the seasons. Data used are percent composition of stomach contents transformed using an arcsin square-root function. MANOVA was used to test the hypothesis that season was a significant source of diet variation. Specific F-tests to contrast means for each pair of seasons were used to make multiple comparisons.

Species	Independ. variable	Manova results (Wilks' lambda)		Dependent variables	Univariate results			Contrast summary**
		F-value	p-value		F-value	p-value	df	
<i>Floridichthys carpio</i>	season	1.95	0.0101	amphipods	1.32	0.2672	3/319	
				copepods	2.52	0.0581	3/319	
				ostracods	3.28	0.0213	3/319	all>sum
				nematodes	1.91	0.3122	3/319	
				forams	0.85	0.4672	3/319	
<i>Eucinostomus harengulus</i>	season	3.34	0.0032	amphipods	4.20	0.0062	3/319	win&spr>sum&fall
				algae	0.61	0.6070	3/171	
<i>Fundulus grandis</i>	season	1.33	0.1745	amphipods	6.09	0.0006	3/171	spr>all
				leopods	1.60	0.1896	3/245	
				fish (unidentified)	0.17	0.6823	3/245	
				insects (terrestrial adults)	0.05	0.8272	3/245	spr>all
				algae	3.11	0.0272	3/245	
<i>Lutjanus griseus</i>	season	1.25	0.2232	amphipods	1.80	0.1482	3/245	
				crabs	0.82	0.4858	3/73	
				leopods	3.56	0.0183	3/73	all>win
				insects	1.23	0.3056	3/73	
				fish (unidentified)	0.13	0.5365	3/73	
<i>Strongyura nodata</i>	season	3.03	0.0001	amphipods	0.13	0.7191	3/73	
				leopods	0.84	0.4757	3/73	
				shrimp	1.59	0.1907	3/312	
				ants	4.40	0.0048	3/312	win>all
				insects (terrestrial adults)	2.17	0.0914	3/312	
<i>Sphyræna barracuda</i>	season	1.21	0.2691	fish (unidentified)	1.74	0.1589	3/312	
				amphipods	6.16	0.0004	3/312	spr>all
				eggs	0.93	0.4287	3/312	
				Cyprinodontids	0.55	0.6491	3/60	
				fish (unidentified)	1.65	0.1864	3/60	
					1.94	0.1333	3/60	
					0.97	0.4110	3/60	
					0.76	0.5215	3/60	

* Model degrees of freedom / error degrees of freedom

** If no contrast is indicated, no significant differences occurred.

all year except in winter, when they were seldom consumed. For both *Fundulus grandis* and *Strongylura notata*, adult insects, a prevalent item, were greater in diets in the spring.

Discussion

Shared Resources

As commonly occurs in aquatic habitats, diets overlapped among the 6 species as resources were often shared (Harrington & Harrington 1961, Livingston 1982, Odum 1983). This overlap occurred in all areas and throughout the study period.

Diet overlap can become particularly evident when one resource attains a periodic peak of abundance. In other aquatic habitats, for example, populations of penaeid shrimp (Salini et al. 1990) or larval insects (Harrington & Harrington 1961) increase under certain conditions, and opportunistic fish take advantage of the resource abundance. A similar seasonal increase in exploitation of a particular food resource was found in the current study for adult insects exploited by *Fundulus grandis* and *Strongylura notata*.

In western Florida Bay, gray snapper and spotted sea trout (*Cynoscion nebulosus*) diets overlapped when peak abundances of pink shrimp (*Penaeus duorarum*) occurred in November (Hettler 1989). Although a similar pattern might have been expected in the current study, none became evident. Migrating juvenile pink shrimp, while a major

portion of the epibenthic fauna in western Florida Bay, have lower densities in the interior and eastern Bay (Holmquist et al. 1989a).

Diet Breadth and Variability

Three types of feeding strategies were identified among the 6 species based on diet breadth and degree of opportunism. Firstly, *Floridichthys carpio* and *Eucinostomus harengulus* appeared to rely strongly on the plasticity of their diets, feeding on one basic resource consistently, but also consuming smaller quantities of many other resources. Although it was not separated from other materials in the unrecognizable category, these species probably consumed detritus. A product of breakdown of dead plants, this material contains a "coating" of bacteria and fungi of nutritional value (Heald et al. 1974). Primary consumers of detritus include amphipods, shrimp, crabs, and certain fishes. Among the 6 species analyzed in this study, a major portion of the diet of *Floridichthys carpio* was probably composed of detritus; in the North River, the diet of this killifish was 21% detrital material (Odum 1971). In that study, *Eucinostomus harengulus* was considered a secondary consumer of this material, with only 6% of the gut contents directly composed of detritus (Odum 1971).

The second major strategy was employed by *Fundulus grandis*, *Lutjanus griseus* and *Strongylura notata*. Rather than switching among a very wide variety of items, they consumed about 5 items consistently and abundantly. Thus,

these fishes tended to rely more strongly on omnivory, or constant foraging for these several items, rather than opportunism. The diets of *Fundulus grandis* probably also included detritus (Rozas & LaSalle 1990). However, the 3 other species analyzed in this study were apparently not direct consumers of detritus (deSylva 1963, Odum 1971, Starck & Schroeder 1971, Brook 1977, Thayer et al. 1987a).

The third major strategy was exemplified by the piscivore, *Sphyraena barracuda*. One resource, fish, was consistently and effectively targeted by the barracuda.

These modes of feeding are consistent with other estuarine investigations. Two extreme modes of feeding were identified in Lake Ponchartrain, for example, with detritivore/omnivores, such as mullet, on one end of the spectrum, and piscivore/specialists, such as gar and jacks, on the other end (Darnell 1961). Similar extremes were observed in a red mangrove/saltmarsh habitat in east Florida, with killifish and snook at opposite poles (Harrington & Harrington 1961). In these examples, intermediate strategies incorporate the consumption of small benthic invertebrates in diets with greater and lesser portions of detritus and fish. In the current study, the detritivore was probably most strongly represented by *Floridichthys carpio*, with the barracuda at the opposite extreme. Intermediate species include the mojarra, *Fundulus grandis*, *Lutjanus griseus* and *Strongylura notata*, in order of increasing piscivory.

Influence of the Salinity Gradient

Diets of three species were significantly influenced by location along the salinity gradient. *Eucinostomus harengulus* and *Floridichthys carpio* diets included more algae upstream and more copepods, ostracods, and nematodes downstream. This finding tends to be consistent with the reduced levels of benthic invertebrate populations found upstream in a previous investigation in northeastern Florida Bay (Montague et al. 1989). Plant materials, other than seeds, are generally less concentrated energy sources than animal sources (Odum 1983).

Lutjanus griseus consumed more crabs up- than downstream. Although all the parts were not identified to species in the current study, most were probably from mud crabs of the species *Rhithropanopeus harrisi*. This brackish water crab was abundantly collected in minnow traps placed in mangrove shorelines upstream, but was never collected downstream (unpublished data). It occurred abundantly in the gray snapper stomachs in the North River (Odum 1971). *Rhithropanopeus harrisi* is, thus, an important forage item for snappers that appears to occur abundantly in brackish water in the study area. As mean salinity rose from 16 to over 30 ppt in northeastern Florida Bay, these crabs were virtually eliminated from seagrass beds over a period of four years (Holmquist et al. 1989a).

Crabs in general may not be readily assimilated as food by fishes due to a higher percentage of exoskeleton

(Weisberg & Lotrich 1982). In an experiment, *Fundulus heteroclitus*, fed a diet of only fiddler crabs (*Uca pugnax*) lost weight (Weisberg & Lotrich 1982). In a salt marsh where fiddler crabs comprised 17 times more food volume than any other item for *Fundulus grandis*, the killifish may have compensated for the crabs' low caloric value by consuming their prey in very large quantities (Rozas & LaSalle 1990).

Since two items consumed more abundantly upstream, algae and crabs, were lower quality energy sources for fish growth, these locations may be somewhat lower quality habitats than mid- and downstream in terms of obtainable foods for these species. The fishes that forage upstream may compensate, however, by foraging on greater quantities of the lower quality items that are available.

CHAPTER 5
PREDATION RATES ON SMALL BENTHIC FISH
ACROSS A SALINITY GRADIENT

The value of estuaries as nursery areas for fishes that have wider distributions as adults has been confirmed in many studies (e.g. Gunter 1938, Reid 1954, Carter et al. 1973, Blaber & Blaber 1980, Yanez-Arancibia et al. 1980, Bell et al. 1984, Blaber et al. 1985, Blaber et al. 1989, Pinto 1987, Robertson and Duke 1987). An influx of juveniles to an estuary usually coincides with the season of highest freshwater discharge, when salinity levels drop. As juveniles develop in the estuary, they tend to migrate from fresher upstream areas to more saline downstream habitats (Weinstein 1979, Rogers et al. 1984). Based on observations such as these, one of the paradigms of estuarine ecology has developed: that estuarine salinity conditions contribute to the survival of juvenile fish because stenohaline marine predators are precluded from entering portions of the estuary having lower, more variable conditions of salinity (Gunter 1961, Austin 1971, Browder & Moore 1981, Odum et al. 1982). Despite its widespread acceptance, this hypothesis has not been tested before now.

Predation is one of the most complex of the species interactions studied by ecologists. In comparing levels of predation intensity among habitats, not only are relative abundances of predators and prey important factors, but the potential rates of predation must also be estimated (Kitching 1983). These rates depend on behavior of predator and prey and characteristics of the habitat. Some behavioral and microhabitat aspects have been modeled by observing individual components of predator/prey interactions in the laboratory (e.g. Holling 1966; Barshaw and Able 1990a). Other habitat related factors, however, must be measured in the field, and are thus, more difficult to determine.

The tethering technique, a useful field method, has increasingly been used by ecologists studying the effects of different habitat features on predator/prey interactions. Briefly, the tethering technique involves affixing a line to a prey organism so that evidence of predation can be determined from its condition after a period of time. These investigations are usually accompanied by complementary laboratory studies or censuses of predators and prey. A summary of tethering studies is presented in Table 5-1.

In this study, the tethering technique has been used to compare predator encounter rates across a gradient of salinity conditions. The question of interest is, are these rates lower in the more variable upstream locations relative to mid- and downstream where conditions remain more saline?

Table 5-1. Summary of studies testing predation hypotheses in aquatic habitats using tethering techniques.

Hypothesis Tested	Taxa Tethered			
	Decapod Crustaceans	Brittlestars	Fish	Mangrove Leaves and Propagules
Comparison of predator encounter rates among macro-habitats	Heck & Wilson 1987 Wilson 1989	Aronson 1989	Shulman 1985 McIvor & Odum 1988 THIS STUDY	Smith 1987
Prey vulnerability in and out of vegetated micro-habitats	Barshaw & Able 1990a Barshaw & Able 1990b Hay et al. 1989 Heck & Thoman 1981 Herrnkind & Butler 1986 Wilson 1989 Wilson et al. 1987 Wilson et al. 1990		Rozas & Odum 1988	
Absolute rate of predation				Robertson 1987 Smith 1987
Modification of prey behavior by the presence of predators			Power & Matthews 1983 Phillips & Swears 1979	
Preference by predators for a particular prey		Aronson 1988		Smith 1987

This experiment actually integrates several of the steps involved in predation that were described by Holling (1966). First, measurements indicate whether or not predators occur in the locations under comparison. Secondly, the tests indicate how well the predators can perceive the prey, given the conditions at the site (e.g. turbidity levels). Thirdly, the ability and propensity to consume particular prey species relative to size and palatability is indicated.

To add to the understanding of the influence of freshwater inflow on fish assemblages, the objective of this chapter was to compare predator encounter rates up- and downstream during the rainy season. If the paradigm is true, fewer tethered prey should be consumed upstream than downstream, as the marine predators are excluded from these locations due to the lower, more variable salinity conditions.

Materials and Methods

Preliminary Tests

To evaluate the effectiveness of the tethering technique for specific prey fishes and conditions in the study area, preliminary tests were conducted within an enclosure formed from two 30 m seine nets that excluded all potential predators. For these tests, fish were tethered by sewing one end of a 1.0 m length of 8 lb test monofilament

fishing line through the lower jaw of a small fish (4-10 cm). The other end was looped over a 1.25 cm diameter polyvinylchloride (PVC) pole that had been driven into the substrate. Sixteen fish were tethered inside each enclosure and checked at 3, 6 and 24 hour intervals. Although all fish survived and remained securely tethered for three hours, in these preliminary tests, one (*Eucinostomus gula*) died after six hours and several other fishes died after 24 hours (Table 5-2). In addition, fish that died at the bottom were quickly attacked by scavengers (e.g. crabs and gastropods), possibly interfering with interpretation of test results.

Since the study objective was to determine rates of prey encounters with predators, not scavengers, these results prompted further investigation into alternative tether and stake designs. After several prototypes, an L-shaped stake was made by joining two 1.0 m long PVC pipes with an elbow (Figure 5-1). A hole was drilled at the free end for attaching the tethered fish (as above) and the other end was driven into the sediment. When deployed, the top bar of the L-shaped stake was above the surface of the water. To ensure that predators and not scavengers were responsible for removing the prey, the tethered fish were forced to remain above the substrate by adjusting the depth to which the pole was driven into the substrate.

Table 5-2. Results of tests using tethered fish within an enclosure formed by two block nets at Buttonwood Sound. Species used were: *Fundulus grandis*, *Eucinostomus gula*, and *Floridichthys carpio*.

Test number	After 3 hours			After 6 hours			After 24 hours		
	Live	Dead	Missing	Live	Dead	Missing	Live	Dead	Missing
1	16	0	0	15	1	0	8	0	8*
2	16	0	0	16	0	0	14	0	2
3	16	0	0	16	0	0	3	12**	1

* Net partially down overnight; needlefish found inside net

** Fish that had died were being consumed by scavengers (e.g. anemones, gastropods, and crabs)

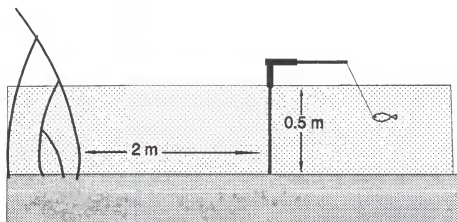


Figure 5-1. Illustration and dimensions of the tethering systems used in this study as deployed near mangrove edges.

Tethering Experiment

Small fish were tethered at far/up-, mid/up-, mid- and downstream locations in two systems (west and east) in northeastern Florida Bay (Figure 5-2). Tethered species included those that are consumed by dominant members of the predator guild in the study area, as indicated by the results of the food habits portion of this overall study (Chapter 4). Small fish make up over 25% of the diets of *Strongylura notata* (redfin needlefish), *Lutjanus griseus* (gray snapper) and *Sphyræna barracuda* (great barracuda).

Trials were conducted on two dates at each of the eight locations during mid-summer 1990. For each trial, salinity, horizontal secchi distance, and water depth were recorded. Fish to be used in each trial were collected by setting out several minnow traps near each site on the day before a test. Small fish (4 to 10 cm total length) from five species were used in the 16 trials: killifish (*Floridichthys carpio*, *Cyprinodon variegatus*, *Fundulus grandis*, and *Fundulus confluentus*) and crested gobies (*Lophogobius cyprinoides*). In each trial, ten to sixteen fish were tethered 10 m apart and about 2.0 m from the mangrove edge (Figure 5-1). Sites with water depths of about 50 cm were selected for each fish. The total time each prey was tethered ranged from 3 to 3.5 hours. For approximately 1.5 hours, while observers were within 10 to 100 m of the tethered stakes, they recorded when possible the type, size, and number of predators that approached or

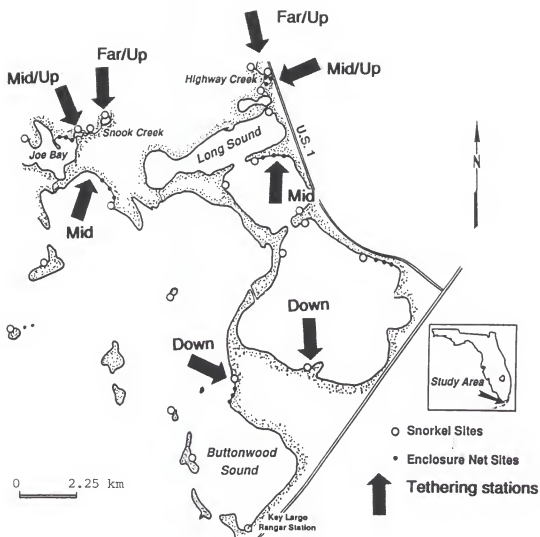


Figure 5-2. Locations of study sites in northeastern Florida Bay.

attacked tethered fish. Other potential predators in the vicinity were also noted. At the end of the test period, each stake was examined. Predation was assumed to have occurred if a fish was missing, severely damaged or if a predator was tethered.

Analysis

For each test, the percent of prey that were subjects of predation was used as the dependent variable for statistical analyses. Analysis of variance (SAS GLM) was used to determine if predator encounter rates differed due to gradient position (i.e. far/up-, mid/up-, mid- and downstream) or system (east, west). To make multiple comparisons, specific F-tests were used to contrast means for each pair of gradient positions. SAS GLM with Student-Newman-Keuls multiple comparison tests were also used to determine if tethering different species created an extraneous source of variation.

In addition, correlations were calculated between the predator encounter rates and corresponding ranges of visibility (horizontal secchi distance), salinity, and water depth. ANOVA was also used to determine if differences in salinity, visibility and water depth were due to gradient position.

Results

Of 235 tethered fish used, a mean of 83.5% were subjects of predation after the 3 to 3.5 hour period (Table 5-3). Predation rates averaged 90% in mid/up-, mid- and

Table 5-3. Results of predator encounter trials comparing rates in four gradient positions from down to far upstream in two systems. Fish were tethered for three hours adjacent to mangrove edges. Trials were conducted from June 20, 1990 to August 3, 1990.

System*	Gradient**	Test Number	Results Total Fish	Percent Missing	Salinity	Secchi distance	Mean Water Depth
1	1	1	16	25	22.5	1.0	64
1	1	2	10	70	23.5	1.5	62
1	2	1	12	100	22.9	1.0	53
1	2	2	15	87	14.7	1.0	52
1	3	1	16	100	52.0	2.2	45
1	3	2	15	100	50.0	1.0	62
1	4	1	16	100	50.0	5.5	58
1	4	2	15	93	45.0	3.4	58
2	1	1	13	77	7.3	2.0	47
2	1	2	15	53	16.0	2.0	48
2	2	1	16	94	29.9	1.0	48
2	2	2	13	100	15.5	1.0	50
2	3	1	16	88	50.0	0.8	62
2	3	2	16	69	48.0	0.8	73
2	4	1	16	93	45.0	4.0	93
2	4	2	15	87	45.0	9.0	93
Total Mean			235	83.5	33.4	2.3	60.8

*Systems: 1 = West, 2 = East

**Gradient: 1 = Far/upstream

2 = Mid/upstream

3 = Midstream

4 = Downstream

downstream locations contrasted to 55% for those far/upstream locations (Figure 5-3). Salinity, range of visibility, and water depth also varied across the gradient (Figure 5-3).

The far/upstream predation rate was significantly lower than the rates for the mid/up-, mid-, and downstream locations, but there were no significant differences between east and west systems (Table 5-4). Rates of predation were not significantly different among the species ($df=4$, $F=1.98$, $p=0.1296$).

Neither salinity, secchi distance nor water depth were significantly correlated with observed predator encounter rates (Table 5-5). These factors did vary significantly among the locations, however.

Salinity means were not significantly different between the far/up- and mid/upstream locations ($p<0.3454$, $df=1$), nor between the mid- and downstream locations ($p<0.3921$, $df = 1$). However, the subgroup formed by the far/up- and mid/upstream stations had a significantly lower mean salinity than the subgroup formed by the mid- and downstream locations ($p<0.0001$ for each pair of contrasts).

Range of visibility was significantly greater downstream than at the other locations ($p<0.005$ for each pair of contrasts). Water depth, however, was significantly greater at the downstream/east location ($p<0.05$ for each pair of contrasts).

Predator Encounter Rates

Mean and Standard Deviation

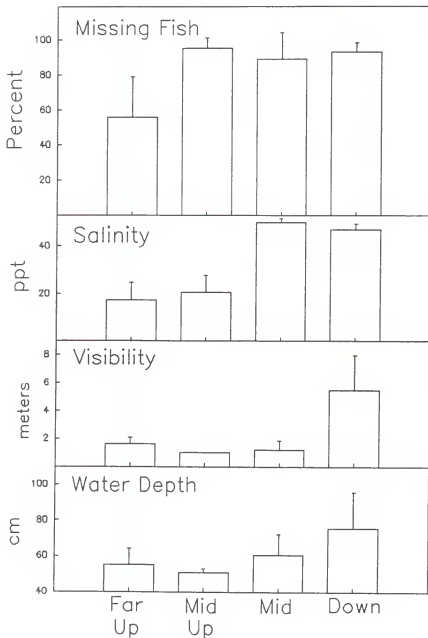


Figure 5-3. Mean predation rates for small (<10 cm TL) benthic forage fish tethered for 3 hours across a salinity gradient in northeastern Florida Bay. Error bars indicate the standard deviations of test rates resulting from 4 tests in each of the 4 gradient positions.

Table 5-4. Analysis of sixteen predator encounter rate tests. Data used are percentage of fish missing (arcsine-transformed) after being tethered for three hours adjacent to mangrove edges. ANOVA was used to test the hypothesis that gradient and system were significant sources of variation. Specific F-tests to contrast means for each pair of gradient positions were used to make multiple comparisons.

Source of Variation	F-value	p-value	df*	Contrast Summary** ($p < .01$)
MODEL	4.06	0.0332	7/8	
Gradient	6.94	0.0129	3/8	1 < 2, 3 & 4
System	1.12	0.3206	1/8	No differences
Gradient X System	2.22	0.1634	3/8	No differences

* Model degrees of freedom / Error degrees of freedom

** Gradient: 1 = Far/upstream; 2 = Mid/upstream; 3 = Midstream; 4 = Downstream

Table 5-5. Correlations of predator encounter rates with environmental variables. Data are percentage of fish missing (arcsine transformed) after being tethered for three hours adjacent to mangrove edges in 16 trials. Pearson correlation coefficients and probability values are indicated.

Variable	Test Results	
	Correlation Value (R)	p-value
Mean Water Depth	-0.1463	0.5885
Salinity	0.3688	0.1597
Secchi Distance	0.1308	0.6293

Thus, although the predator encounter rate was greater at the two far/upstream locations, salinity, visibility, and water depth were not unusual at these locations relative to the others. Salinity, the parameter of most interest, was lower at both the far/up- and mid/up- locations, but the rate of predation was lower far/upstream, and higher at the mid/upstream location.

Potential predators that were observed approaching tethered fish at all the locations included redbfin needlefish, gray snapper, and barracuda (Table 5-6). Observed only in the far/upstream locations were bull shark juveniles, gar, alligators, and turtles.

A total of 28 actual predation events were recorded in which the attacking predator could be identified (Table 5-6). Most of these events (22) were due to needlefish (*Strongylura notata*), half of which became tethered themselves. Once they had swallowed the prey, the needlefish were unable to cut the fishing line with the teeth on their elongated jaw, but they usually were eventually able to work the prey and themselves free of the tether (e.g. by leaping).

Discussion

Predator encounter rates averaged more than 50%, even in the most upstream locations. Thus, piscivorous predators are ubiquitous along the estuarine gradient and were effective at consuming tethered prey throughout the system.

Table 5-6. Species of predators associated with encounter rate experiments. Observers in the boat or water recorded the following predators taking, or in the vicinity of, the tethered fish.

Species	Predation Events Observed	Estimated Abundance In Vicinity of Tethers	Estimated Size cm.	Gradient* Where Observed
<i>Negaprion brevirostris</i>	3	6	70-125	2,3
<i>Carcharhinus leucas</i>		1	75	1
<i>Strongylura notata</i>	22	1000+	15-32	1,2,3,4
<i>Centropomus undecimalis</i>		10+	45-75	2,3,4
<i>Epinephelus itajara</i>		1	75	4
<i>Caranx hippos</i>	2	30+	45-50	1,4
<i>Lutjanus griseus</i>		100+	15-40	1,2,3,4
<i>Haemulon sciurus</i>		100+	15-40	4
<i>Lepisosteus platyrhincus</i>		16	45-55	1
<i>Sphyræna barracuda</i>	1	30+	15-70	1,2,3,4
<i>Trionyx ferox</i>		1	45	1
<i>Alligator mississippiensis</i>		2	180-200	1
<i>Butoroides striatus</i>		1		1

* Gradient: 1= Far/Upstream, 2=Mid/Upstream, 3=Midstream, 4=Downstream

In all study locations, these predators included euryhaline species (e.g. snook, needlefish, gray snapper, crevalle jacks, juvenile barracuda). Upstream, they were joined by freshwater species such as gar that can forage in brackish conditions. Similarly, lemon sharks are primarily marine predators that were also observed upstream.

A relatively straightforward hypothesis can be given to explain the finding that a great number (90%) of the tethered fish were subject to predation in the mid- and downstream locations. Greater predator encounter rates are associated with proximity to some type of structurally massive habitat such as a rocky breakwater (Aronson 1989) or coral reef (Shulman 1985). Similarly, findings in Chapter 3 indicate that where mangrove habitat is more developed (i.e. greater tree height, fringe width, canopy cover) greater abundances of large roving fish occur; this fish group includes many of the predators occurring in the study area. In addition, habitat development is significantly greater in mid- and downstream locations. Thus, the greater encounter rates found further downstream may be explained by the attraction of large roving predators to the structure associated with well-developed mangrove habitats.

While attraction to highly developed mangrove habitats may explain why predation rates were so high at mid- and downstream locations, it does not account for the high rate of predation that was also found at the mid/upstream locations. In previous chapters, findings indicate that in

upstream locations overall, large roving fish densities are lower (Chapter 2). Conditions upstream overall may be inhospitable for large roving fish, preventing them from permanently residing in these locations (Chapters 3 and 4). In addition, salinity regime in both the far/up- and mid/upstream locations, was low and variable in the current study. Based on these findings, one would have expected the experiments to indicate lower predator encounter rates at both the far/up- and mid/upstream locations.

However, in actuality, tethered fish suffered lower rates of predation far/upstream than mid/upstream. Thus, the abundance of predators was probably equivalent at mid/up-, mid-, and downstream locations, but less abundant at far/upstream locations. The predator encounter rates, therefore, do not appear to simply be functions of salinity regime or mangrove habitat development alone.

One hypothesis that could explain the greater rates mid/upstream in comparison to far/upstream, could be that a significant number of the stenohaline predators primarily residing in marine habitats also temporarily forage at the edge of their primary range (e.g. Weinstein 1979). The mid/upstream locations would be at the edge of this range for marine predators. An analogous situation may occur for freshwater predators at the other side of the marine/freshwater interface.

To explain the lack of predators far/upstream, perhaps other characteristics of these locations (besides

salinity regime and mangrove habitat development) make them safer havens for small benthic fishes. In contrast to all the other locations, to forage far/upstream, a predator would have to negotiate a series of sinuous channels and interspersed ponds. Shallow shoals occur at pond/creek intersections that are sometimes only a few centimeters deep. This complex system seems likely to prevent access by casual foragers and predators above certain size limits.

Based on these results, the ecological paradigm may thus be qualified. Large predators may be prevented from permanently occupying upstream locations by low and variable salinity conditions, and the complexity of sinuous channels may prevent them from foraging in far/upstream locations. A safe haven for small benthic fish thus occurs in complex habitats at the marine/freshwater interface. These findings tend to support the hypothesis suggested by Browder & Moore (1981): ideal juvenile fish habitat may occur where the variable salinity conditions overlap areas of such habitat complexity. They tend to refute, however, the hypothesis that small fishes are protected from predation in estuaries by lower salinities which tend to exclude stenohaline marine predators.

CHAPTER 6 IMPLICATIONS AND CONCLUSIONS

Implications for Mangrove Fish Ecology

Fish and Mangrove Shorelines

Mangrove shorelines fulfill the food and cover habitat requirements for many fishes. Among the functional roles of inter-tidal mangroves as habitats for fish, the best established is that of a temporary feeding location for a wide range of species (Robertson & Duke 1990a, Blaber et al. 1985, Morton 1990). These species include small schooling planktivores, benthic forage fish, and large piscivores. They spend periods of low tide in deep open water or shallow ponds and feed in the mangroves when the tide inundates the forest (Davis 1988).

Since northeastern Florida Bay is non-tidal, the mangrove habitats are unlike those in many other areas. In Florida Bay permanently inundated mangrove habitats are believed to provide young fish with refuge from larger predators (Thayer et al. 1987a). This role was supported in the current study, particularly for larger juveniles of the

estuarine transient species, *Lutjanus griseus* and *Haemulon sciurus*. Of the habitats within Florida Bay, these species prefer mangroves during the day (Thayer et al. 1987a & 1987b). An important aspect of habitat use by these species is their migration away from the mangrove shorelines at night, to feed in nearby seagrass beds (Starck & Schroeder 1971, Sogard et al. 1989c). Thus, in both tidal and non-tidal habitats, linkages between mangrove shorelines and other habitats may be critical for diel behavior patterns.

Besides snappers and grunts, other species that may similarly rely on both mangroves and seagrass beds include snook, sheepshead, barracuda and nurse sharks. A common life history pattern occurs among these fishes: recruitment from offshore as post-larvae, settlement and growth in inshore habitats, and movement back offshore or to deeper water as they attain larger size classes (Starck & Schroeder 1971, DeSylva 1963, Jennings 1985). These fishes tend to use seagrass beds when they are smaller and move to mangroves when they attain larger juvenile sizes.

Thus, shallow water habitats including mangroves and seagrass beds, may be linked to one another through such behavioral and life history patterns (Odum et al. 1982, Parrish 1989). Mangroves provide cover and food resources that are very different from adjacent habitats dominated by submerged aquatic vegetation (SAV). However, both types of habitats appear to be necessary to support certain fish species. Prime locations for supporting these species may

occur where both mangrove development and SAV are greater. Reduced SAV may thus account for the reduced abundance of large roving fish upstream.

Selection Among Mangrove Habitats

Mangrove shorelines vary in functional value depending on the degree of development and habitat needs of the fishes. In freshwater streams, a gradient model has been proposed (Schlosser 1987) that appears to apply equally well in northeastern Florida Bay. This model identifies a gradient from upstream areas (environmentally unstable, shallower, lesser habitat development) to downstream areas (stable, deeper, greater development). Greater habitat development is linked with the occurrence of more species and larger piscivorous individuals (Schlosser 1987). For smaller fishes, upstream areas provide refugia from larger piscivores that are more abundant downstream.

In northeastern Florida Bay, the mangrove habitats ranged from less developed upstream (small trees, narrow fringe, shallow water, high environmental variability), to more developed downstream (tall trees, deeper water, environmentally more stable). Among the large roving species, greater abundances of gray snappers and grunts were associated with more developed mangrove habitats in the current study. In addition, numbers of species of large roving fish were more abundant downstream than upstream. Thus, in terms of large roving fish, the model applies well to northeastern Florida Bay.

For smaller fishes, the implications of the model are that upstream habitats are occupied by colonizing fishes. Competition for food resources limits the abundances of these fishes more than predation. Downstream, predation is a more powerful force in the community structure. Thus, upstream areas should be relatively advantageous for small fishes in both freshwater streams and estuarine habitats.

Small fishes, however, were not more abundant upstream in northeastern Florida Bay. Young-of-the-year estuarine transient juveniles may represent the colonizers described in the model. However, these fishes were absent in the current study. Thus, there appears to be a missing component of the fish community in the study area, particularly in the upstream fish assemblages in the current study.

Implications For Estuarine Fish Ecology:
The Nursery-ground Hypothesis

The absence of young-of-the-year juveniles of estuarine transient fishes in the study area was also a significant departure from the results one would have expected based on widely accepted theories in estuarine ecology. In northeastern Florida Bay, this condition was not unique to the mangroves; both seagrass and mangrove habitats in eastern and central Florida Bay also have low populations of very young transients (Sogard et al. 1987, 1989as, Thayer et al. 1987a).

The potential pool of post-larval estuarine transient species from the Atlantic Ocean and Gulf of Mexico includes sciaenids, lutjanids, haemulids, centropomids and elopids. Presumably, currents carry potential recruits to the northeastern Florida Bay area. Exchange with these sources is limited in northeastern Florida Bay due to the presence of the Keys and western mudbanks. Internal circulation in Florida Bay is also weak due to the many islands and lack of tides. If post-larval transients do enter the northeastern Bay, they may meet with significant predation pressure due not only to the occurrence of piscivores but also to a reduction in the cover afforded by seagrass beds, which tend to become less developed in the eastern Bay. These conditions indicate that the chances of post-larval forms reaching the upstream locations in the study area may be small. Such conditions may not be unusual in estuaries, however.

Habitat conditions documented in this study for the upstream locations included almost no SAV and reduced mangrove habitat development. However, shallow ponds and sinuous creeks upstream may effectively reduce predator encounter rates. Thus, a key factor in improving the use of upstream habitats by estuarine transient juveniles appears to be the presence of a persistent abundance of SAV.

Management Implications

Northeastern Florida Bay may have historically supported more estuarine transient juveniles and greater

densities of fish than was observed in the current study. Higher, abruptly changing salinity conditions may somehow inhibit the development of lush communities of submerged aquatic vegetation that provide cover for small fish and benthic invertebrates (Montague et al. 1989). Sustained lower salinity periods may promote growth of lush seagrass (*Ruppia maritima*) or algal (*Chara*, *Batophora*) communities (Tabb et al. 1961, Montague et al. 1989). During more saline periods, less dense growth of *Halodule wrightii* communities may develop, if any vegetation grows at all. As salinity changes with seasons, these communities may alternate.

Although the regular study was conducted during a period of very low rainfall and can only serve to provide information on the ecosystem under low freshwater inflow conditions, the pilot study took place at a time of higher rainfall and high freshwater inflow conditions (summer 1988). In the pilot study, from October 1988 through March 1989, in upstream habitats, extremely dense *Ruppia* and algal communities were observed. With experimental traps and gill nets, great numbers of fishes were collected including gray snappers, jacks, catfish and cichlids. A small mangrove island and its surrounding waters in the Joe Bay study area were heavily used by white pelicans (fish eating birds). However, during the regular study (May 1989 - May 1990), very little *Ruppia* was observed. The pelican island was evidently never used by birds and because the traps no

longer captured many fish, their use was abandoned. This evidence indicates that the *Ruppia* community was probably supporting a greater fish population in the area than observed at any time during the course of the regular study.

Thus, northeastern Florida Bay, in the drought year recorded in this study, was unusual in comparison to other tropical, subtropical and warm temperate estuaries. Water management efforts may be needed to restore sustained low salinity periods, thereby inducing greater submerged aquatic vegetation development and greater influx of estuarine transient juveniles upstream into the more protected habitats.

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BIOGRAPHICAL SKETCH

Janet Ann Ledtke Ley was born 11 June, 1951, in Detroit, Michigan, to Frederick G. and Helen M. Ledtke. Janet graduated from Rochester High School, Rochester, Michigan, in 1969. She received her Bachelor of Science degree in resource development at Michigan State University, East Lansing, Michigan, in 1973.


Janet devoted ten years to environmental planning for the Pinellas County government, in Clearwater, Florida, from 1974 through 1984. While working as a planner, in 1979, she earned her Master of Science degree at the University of South Florida. Her thesis was entitled "Exploring Transfer of Development Rights," a concept that was later incorporated into her work on Pinellas County's plan for environmental protection of wetland ecosystems. Janet worked as a consultant for the Tampa office of Dames & Moore during 1985.

In 1986, Janet enrolled in the Ph.D. program in systems ecology, in the College of Environmental Engineering Sciences, at the University of Florida, Gainesville, Florida. In May 1992, Janet received her Ph.D., and hopes to continue to work in ecosystems research.

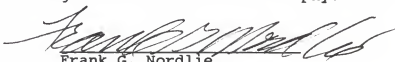
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Clay L. Montague, Chairman
Associate Professor of
Environmental Engineering Sciences

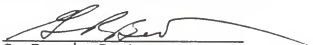
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Carole C. McIvor, Cochairman
Assistant Professor of
Forest Resources and Conservation

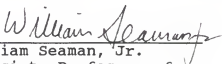
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Frank G. Nordlie
Professor of Zoology

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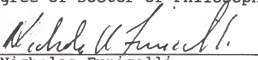

G. Ronnie Best
Scientist
Environmental Engineering Sciences

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William Seaman, Jr.
Associate Professor of
Forest Resources and Conservation

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Nicholas Funicelli
Assistant Professor of
Forest Resources and Conservation

This dissertation was submitted to the Graduate Faculty of the College of Engineering and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

May 1992



Winfred M. Phillips
Dean, College of Engineering

Madelyn M. Lockhart
Dean, Graduate School